2.1.3. Mallard (surface-feeding ducks)

Order Anseriformes, Family Anatidae. Surface-feeding ducks are the most familiar ducks of freshwater and saltwater wetlands. They feed by dabbling and tipping up in shallow water, often filtering through soft mud for food. They feed primarily on seeds of aquatic plants and cultivated grains, although they also consume aquatic invertebrates, particularly during the breeding season (Jorde et al., 1983; Swanson et al., 1985). All species have a bright colored patch of feathers on the trailing edge of each wing, and the overall plumage of the males is more colorful than that of the females. Dabbling ducks range in size from the green-winged teal (average 37 cm bill tip to tail tip) to the northern pintail (average 66 cm).

Selected species

The mallard (*Anas platyrhynchos*) feeds mostly on aquatic plants, seeds, and aquatic invertebrates, depending on the season, and forages in ponds and wetlands by dabbling and filtering through sediments. It is widespread throughout most of the United States and is the most abundant of the United States ducks (USFWS, 1991). In the past decade, however, its numbers have declined markedly across its principal range in the mid-continental region because of habitat degradation and drought (USFWS, 1991). Mallards interbreed with domestic ducks and black ducks (*Anas rubripes*).

Body size. Mallards average 58 cm from bill tip to tail tip. Male mallards are generally heavier than females (Delnicki and Reinecke, 1986; Whyte and Bolen, 1984; see table). Female mallards lose weight during the laying and incubation periods; males lose weight from their spring arrival through the peak of the breeding season and then gain weight while the females are incubating (Lokemoen et al., 1990a).

Habitat. Wintering mallards prefer natural bottomland wetlands and rivers to reservoirs and farm ponds (Heitmeyer and Vohs, 1984); water depths of 20 to 40 cm are optimum for foraging (Heitmeyer, 1985, cited in Allen, 1987). The primary habitat requirement for nesting appears to be dense grassy vegetation at least a half meter high (Bellrose, 1976). Mallards prefer areas that provide concealment from predators such as seeded cover (fields established on former croplands) (Klett et al., 1988; Lokemoen et al., 1990b), cool-season introduced legumes and grasses (Duebbert and Lokemoen, 1976), and idle grassland with tall, dense, rank cover in the area (Duebbert and Kantrud, 1974). Nests usually are located within a few kilometers of water, but if choice nesting habitat is not available nearby, females may nest further away (Bellrose, 1976; Duebbert and Lokemoen, 1976).

Food habits. In winter, mallards feed primarily on seeds but also on invertebrates associated with leaf litter and wetlands, mast, agricultural grains, and to a limited extent, leaves, buds, stems, rootlets, and tubers (Goodman and Fisher, 1962; Heitmeyer, 1985, cited in Allen, 1987). In spring, females shift from a largely herbivorous diet to a diet of mainly invertebrates to obtain protein for their prebasic molt and then for egg production (Swanson and Meyer, 1973; Swanson et al., 1979; Swanson et al., 1985; Heitmeyer, 1988b). Laying females consume a higher proportion of animal foods on the breeding

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grounds than do males or nonlaying females (Swanson et al., 1985). The animal diet continues throughout the summer, as many females lay clutches to replace destroyed nests (Swanson et al., 1979; Swanson et al., 1985). Ducklings also consume aquatic invertebrates almost exclusively, particularly during the period of rapid growth (Chura, 1961). Mallards concentrate in wetlands at night, apparently feeding on emerging insects (Swanson and Meyer, 1973). Flocks may feed in unharvested grain fields and stubble fields during fall and winter (Dillon, 1959). During periods of food shortage, fat reserves are used as an energy source. During breeding, females continue to feed but also use fat to meet the demands of egg production; females may lose 25 percent of their body mass (in fat) during laying and early incubation (Krapu, 1981).

Molt. Female mallards molt into basic plumage in late winter or early spring, except for the wing molt, which is delayed until about the time broods are fledged. In males, head-body-tail molt commences in early summer and overlaps or is followed by the wing molt. Mallards generally are flightless for about 25 days during the wing molt (Palmer, 1976).

Migration. Although the mallard winters in all four waterfowl flyways of North America (i.e., Pacific, Central, Mississippi, and Atlantic), the Mississippi flyway (alluvial valley from Missouri to the Gulf of Mexico) contains the highest numbers (Bellrose, 1976). Human creation and alteration of water bodies and plant communities have changed the migration and wintering patterns of mallards; in North America the ducks winter farther north than in the past (Jorde et al., 1983). Mallards tend to arrive at their wintering grounds in the Mississippi Valley in mid-September through early November and depart for their northerly breeding grounds again in March (Fredrickson and Heitmeyer, 1988). Adult females that reproduce successfully are likely to return to the same nesting ground the following year (Lokemoen et al., 1990a, 1990b).

Breeding activities and social organization. Older females arrive at breeding grounds earlier than yearling birds, which probably increases their chances of reproductive success because they can select the best nest sites (Lokemoen et al., 1990b). First clutches are generally finished by mid-April in the southern part of the breeding range and late April to May in the northern United States (Palmer, 1976). High rates of nest failure require females to renest persistently to reproduce successfully (Swanson et al., 1985). Average clutch size decreases as the season progresses because the clutch size of renesting females is smaller than initial clutches (Eldridge and Krapu, 1988; Lokemoen et al., 1990b). Older females produce larger clutches than do yearlings (Lokemoen et al., 1990a). Mallards mate for one breeding season, and males typically leave the females at the onset of incubation (Palmer, 1976). Females remain with the brood until fledging. Mallards are serially monogamous and thus remate annually (Palmer, 1976).

Home range and resources. Each pair of mallards uses a home range, and the drake commonly establishes a territory that he defends against other mallards (Bellrose, 1976). Home-range size depends on habitat, in particular the type and distribution of water habitats (e.g., prairie potholes, rivers), and population density (Bellrose, 1976; Dwyer et al., 1979; Kirby et al., 1985).

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Population density. Mallard densities during the breeding season are positively correlated with availability of terrestrial cover for nesting and with availability of wetlands and ponds that provide the aquatic diet of mallards (Pospahala et al., 1974). Availability of suitable wetland habitat for breeding and wintering depends on environmental conditions (e.g., rainfall) (Heitmeyer and Vohs, 1984; Lokemoen et al., 1990a). Average densities of breeding mallards in the prairie pothole region range from 0.006 to 0.67 pairs per hectare (Duebbert and Kantrud, 1974; Duebbert and Lokemoen, 1976; Kantrud and Stewart, 1977; Lokemoen et al., 1990b). Mallards attain their highest densities in prairie and parkland of the southern prairie provinces and in the Cooper River and Athabasca River deltas of Canada (Johnson and Grier, 1988).

Population dynamics. Nest success or failure is an important factor affecting mallard populations. Mammalian predation is the main cause of nest failure, followed by human disturbance (e.g., farming operations) and adverse weather conditions (Klett et al., 1988; Lokemoen et al., 1988). Mammalian predators include fox, badger, and skunk; crows also prey on mallard nests (Johnson et al., 1988). Mallards usually renest if the first nest fails (Palmer, 1976). Juvenile survival depends on food and preferred habitat availability, factors that in turn are affected by environmental conditions. For example, high rainfall is related to increased wetland area, which is positively correlated with duckling growth (Lokemoen et al., 1990a). Annual adult mortality rates vary with year, location, hunting pressure, age, and sex. Females suffer greater natural mortality rates (e.g., typical values of 40 to 50 percent) than do males (e.g., typical values of 30 to 40 percent) (Chu and Hestbeck, 1989). By fall, there is a higher proportion of males than females in most populations (Bellrose, 1976). Immature mortality rates of 70 percent have been recorded in many areas, although lower immature mortality rates are more common (Bellrose, 1976; Chu and Hestbeck, 1989). Annual mortality rates also are greater in areas with higher hunting pressure (Bellrose, 1976).

Similar species (from general references)

- The American black duck (*Anas rubripes*) is only present in the wooded parts of northeastern and north central United States. It nests near woodland lakes and streams or in freshwater and tidal marshes. It is similar in size (58 cm) to mallards using the same habitats.
- The northern pintail (*Anas acuta*) is widespread, occurring in most parts of North America and breeding throughout Canada and the north central United States. Although formerly farily abundant, North American pintail populations have declined dramatically during the past decade (USFWS, 1991). It prefers marshes and open areas with ponds and lakes. Pintails average slightly longer (66 cm) than mallards.
- The gadwall (*Anas strepera*) (51 cm) occurs throughout most of the United States. In Canada, its breeding range is limited to the south central potholes region. It is more common in the west than in the east.
- The American wigeon (*Anas americana*) (48 cm) breeds throughout most of Canada and in the prairie pothole regions of the United States. It winters

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along both the east and west coasts of the United States as well as farther south into Mexico.

- Northern shovelers (Anas clypeata) (48 cm), inhabitants of marshes, ponds, and bays, breed throughout mid to western Canada and the prairie pothole regions of the United States. They winter along the gulf coast, southern Atlantic coast, in Texas, and a few other southwestern states as well as throughout Mexico.
- Blue-winged teal (Anas discors) (39 cm) are fairly common in open country in marshes and on ponds and lakes. Breeding populations occur throughout the central United States and Canada, but wintering populations are restricted to Atlantic and Pacific coastal areas.
- The green-winged teal (*Anas crecca*) (37 cm) is the smallest of the dabbling ducks. *A. c. carolinensis* is the most common subspecies in the United States. It breeds throughout most of Canada and the prairie pothole region of the United States. It overwinters in the southern half of the United States and in Mexico.
- Cinnamon teal (Anas cyanoptera) (41 cm) breeding populations are restricted to the western United States and Mexico, with few reaching southern Canada. Some populations in California and Mexico are year-round residents.

General references

Allen (1987); National Geographic Society (1987); Pospahala et al. (1974); Palmer (1976); Bellrose (1976).

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Mallard Duck (Anas platyrhynchos)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A M A F	1,225 1,043	up to 1,814 up to 1,633	throughout North America	Nelson & Martin, 1953	
	A M winter A F winter	1,246 ± 108 SD 1,095 ± 106 SD		western Mississippi (alluvial valley)	Delnicki & Reinecke, 1986	
	A M winter A F winter	1,237 ± 118 SD 1,088 ± 105 SD		Texas	Whyte & Bolen, 1984	
	A F spring	1,197 ± 105 SD		North Dakota	Krapu & Doty, 1979	
	egg	52.2	32.2 - 66.7	North Dakota	Eldridge & Krapu, 1988	
	at hatching	32.4 ± 2.4 SD		central North Dakota	Lokemoen et al., 1990a	
	B at 3.5 days	32.4 ± 2.4 SD		central North Dakota	Lokemoen et al., 1990b	
	F at 9.5 days F at 15.5 days F at 30.5 days F fledging at 56.0 days	115 ± 37 SD 265 ± 92 SD 401 ± 92 SD 740 ± 115 SD		central North Dakota	Lokemoen et al., 1990b	
	M at 9.5 days M at 15.5 days M at 30.5 days M fledging at 56.0 days	92 ± 12 SD 215 ± 5 SD 460 ± 93 SD 817 ± 91 SD		central North Dakota	Lokemoen et al., 1990b	
Body Fat (g lipid)	A M winter A F winter	174 ± 66 SD 171 ± 56 SD		Texas	Whyte & Bolen, 1984	
	A F April Y F April A F June Y F June	106 ± 34 SD 82 ± 37 SD 22 ± 22 SD 9.6 ± 8.3 SD		North Dakota	Krapu & Doty, 1979	

Factors	Age/Sex/ Cond./Seas.	Mean	Rang (95%	e or CI of mean)	Location	Reference	Note No.
Metabolic Rate (kcal/kg-day)	A F basal A M basal	77 73				estimated	1
	A F winter A M winter	280 220			Texas	Whyte & Bolen, 1984	2
	A F free-living A M free-living	200 192	(94 - (91 -	•		estimated	3
Food Ingestion Rate (g/g-day)							4
Water Ingestion Rate (g/g-day)	A F A M	0.058 0.055				estimated	5
Inhalation Rate (m³/day)	A F A M	0.42 0.48				estimated	6
Surface Area (cm²)	A F A M	1,030 1,148				estimated	7
Dietary Composition					Location/Habitat (measure)	Reference	Note No.
adults: rice jungle rice brownseed pas barnyard grass red rice knot grass signal grass coast cocksput Mamaica sawgt snails other	,			Winter 24 21 19 8.0 8.0 6.5 2.5 1.9 1.3 1.0 6.8	Louisiana/coastal marsh and prairie (% volume; gullet contents)	Dillon, 1959	

Dietary Composition						Location/Habitat (measure)	Reference	Note No.
breeding female (total animal) gastropods insects crustacea annelids misc. animal (total plant) seeds tubers stems	: :	April (67.8) trace 13.1 7.9 38.3 8.5 (32.2) 28.7 2.4 1.1		May (66.8) 24.9 25.6 15.1 0.2 1.0 (33.2) 28.7 4.3 0.2	June (89.4) 16.5 48.1 13.9 10.9 - (10.6) 10.6	south central North Dakota/prairie potholes (% wet volume; esophagus contents)	Swanson et al., 1985	
Population Dynamics	Age/S		Me	an	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	spring A F to A F la spring A F A M	tal ying			307 - 719 38 - 240 40 - 1,44 70 - 1,14	North Dakota/prairie potholes Minnesota/wetlands, river	Dwyer et al., 1979 Kirby et al., 1985	
Population Density (pairs/ha)	A B sp (area A B sp (area	1) oring	0.0		0.006 - 0. 0.031 - 0.	central North Dakota/range of 6 years of data from two different pothole areas	Lokemoen et al., 1990a	
Clutch Size	yearlir A	ng		s ± 1.7 SE .3 ± 1.1 SE	1 - 18	North Dakota/prairie potholes NS/NS	Krapu & Doty, 1979 Bellrose, 1976	
Clutches /Year	if lost	cessful	1		up to 4.5	North Dakota/experimental ponds (nests purposely destroyed) North America/NS	Swanson, unpublished in Swanson et al., 1985 Bellrose, 1976	
Days Incubation			26 25		23 - 29	NS/NS North Dakota/wetlands	Bent, 1923 Klett & Johnson, 1982	8

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Age at Fledging		52 - 60		NS/NS	Bellrose, 1976	
(days)		56		central North Dakota/ potholes	Lokemoen et al., 1990a	
Percent Nests Successful		51 - 61		South Dakota/prairie potholes and fields	Duebbert & Lokemoen, 1976	
ouccessiui		9 - 10		eastern South Dakota/ potholes	Klett et al., 1988	
Number Fledge per Successful Nest		4.9 8.4		NS/NS United States/NS	Cowardin & Johnson, 1979 Bellrose, 1976	9
Age at Sexual Maturity		1 yr		United States/NS	Krapu & Doty, 1979	
Annual Mortality Rates	A M A F	27.2 38.2		eastern-central flyway/NS	Bellrose, 1976	
(percent)	A M fall J M fall A F fall J F fall	40.1 ± 3.1 SE 41.1 ± 7.2 SE 49.9 ± 3.3 SE 48.8 ± 6.0 SE	22 - 51 31 - 59 20 - 72 15 - 68	western mid-Atlantic/NS 1971 to 1985	Chu & Hestbeck, 1989	
	A M fall J M fall A F fall J F fall	39.0 ± 2.3 SE 48.1 ± 5.3 SE 51.5 ± 1.9 SE 56.8 ± 3.2 SE	9 - 60 7 - 69 33 - 64 38 - 68	northeastern United States/NS 1971 to 1985	Chu & Hestbeck, 1989	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early April	May early May	mid-July	CA, UT, MT, SD, NY, VT south central N Dakota	Bellrose, 1976 Krapu & Doty, 1979	
Hatching		June		NW Territory, Canada	Toft et al., 1984	

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Mallard Duck (Anas platyrhynchos)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Molt spring fall	December mid-Sept.		March November	Mississippi Valley	Fredrickson & Heitmeyer, 1988	
Migration spring fall	mid-March mid-October	November	mid-May	arrive north central US leave northern US	Johnson et al., 1987 Palmer, 1976	

- 1 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Nelson and Martin (1953).
- 2 Estimated daily existence energy at 0°C.
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from Nelson and Martin (1953).
- 4 See Chapters 3 and 4 for methods of estimating food ingestion rates from free-living metabolic rate and dietary composition.
- 5 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Nelson and Martin (1953).
- 6 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Nelson and Martin (1953).
- 7 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Nelson and Martin (1953).
- 8 Cited in Palmer (1976).
- 9 Cited in Johnson et al. (1987).

References (including Appendix)

- Allen, A. W. (1987) Habitat suitability index models: mallard (winter habitat, lower Mississippi Valley). U.S. Fish Wildl. Serv. Biol. Rep. No. 82(10.132).
- Bellrose, F. C. (1976) Ducks, geese, and swans of North America. Harrisburg, PA: The Stackpole Co.; pp. 229-243.
- Bellrose, F. C.; Hawkins, A. S. (1947) (cited in Palmer, 1976). Auk 64: 422-430.
- Bent, A. C. (1923) Life histories of North American wild fowl. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 126.
- Brownie, C.; Anderson, D. R.; Burnham, K. P.; et al. (1978) Statistical inference from band recovery data--a handbook. U.S. Fish Wildl. Serv. Resour. Publ. 131.
- Brownie, C.; Anderson, D. R.; Burnham, K. P.; et al. (1985) Statistical inference from band recovery data--a handbook. U.S. Fish Wildl. Serv. Resour. Publ. 156.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Chu, D. S.; Hestbeck, J. B. (1989) Temporal and geographic estimates of survival and recovery rates for the mallard, 1950 through 1985. Washington, DC: U.S. Fish Wildl. Serv. Tech. Rep. No. 20.
- Chura, N. J. (1961) Food availability and preference of juvenile mallards. Trans. N. Am. Wildl. Nat. Resour. Conf. 26: 121-134.
- Coulter, M. W.; Miller, W. R. (1968) Nesting biology of black ducks and mallards in northern New England. Vermont Fish and Game Dept. Bull. 68-2.
- Cowardin, L. M.; Johnson, D. H. (1979) Mathematics and mallard management. J. Wildl. Manage. 43: 18-35.
- Delnicki, D.; Reinecke, K. J. (1986) Mid-winter food use and body weights of mallards and wood ducks in Mississippi. J. Wildl. Manage. 50: 43-51.
- Dillon, O. W. (1959) Food habits of wild mallard ducks in three Louisiana parishes. Trans. North Am. Wildl. Nat. Resour. Conf. 24: 374-382.
- Doty, H. A. (1975) Renesting and second broods of wild mallards. Wilson Bull. 87: 115.
- Duebbert, H. F.; Kantrud, H. A. (1974) Upland duck nesting related to land use and predator reduction. J. Wildl. Manage. 38: 257-265.

2-48 Mallard

- Duebbert, H. F.; Lokemoen, J. T. (1976) Duck nesting in fields of undisturbed grass-legume cover. J. Wildl. Manage. 40: 39-49.
- Dwyer, T. J.; Krapu, G. L.; Janke, D. M. (1979) Use of prairie pothole habitat by breeding mallards. J. Wildl. Manage. 43: 526-531.
- Dzubin, A. (1955) Some evidences of home range in waterfowl. Trans. North Am. Wildl. Nat. Resour. Conf. 20: 278-298.
- Eldridge, J. L.; Krapu, G. L. (1988) The influence of diet quality on clutch size and laying pattern in mallards. Auk 105: 102-110.
- Fredrickson, L. H.; Heitmeyer, M. E. (1988) Waterfowl use of forested wetlands of the southern United States: an overview. In: Weller, M. W., ed. Waterfowl in winter. Minneapolis, MN: University of Minnesota Press; pp. 307-323.
- Fuller, R. W. (1953) Studies in the life history and ecology of the American pintail, *Anas acuta tzitzihoa* (Vieillot), in Utah [master's thesis]. Logan, UT: Utah State Agricultural College.
- Gilmer, D. S.; Ball, I. J.; Cowardin, L. M.; et al. (1975) Habitat use and home range of mallards breeding in Minnesota. J. Wildl. Manage. 39: 781-789.
- Girard, G. L. (1941) The mallard: its management in western Montana. J. Wildl. Manage. 5: 233-259.
- Gollop, J. B.; Marshall, W. H. (1954) A guide to aging duck broods in the field (mimeo). MS: Mississippi Flyway Council Tech. Sect.
- Goodman, D. C.; Fisher, H. I. (1962) Functional anatomy of the feeding apparatus in waterfowl *Aves: Anatidae*. Carbondale, IL: Southern Illinois University Press.
- Heitmeyer, M. E. (1985) Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the upper Mississippi Delta [Ph.D. dissertation]. Columbia, MO: University of Missouri.
- Heitmeyer, M. E. (1988a) Body composition of female mallards in winter in relation to annual cycle events. Condor 90: 669-680.
- Heitmeyer, M. E. (1988b) Protein costs of the prebasic molt of female mallards. Condor 90: 263-266.
- Heitmeyer, M. E.; Vohs, P. A. (1984) Distribution and habitat use of waterfowl wintering in Oklahoma. J. Wildl. Manage. 48: 51-62.
- Johnson, D. H.; Grier, J. W. (1988) Determinants of breeding distributions of ducks. Wildl. Monogr. 100: 1-37.

2-49 Mallard

- Johnson, D. H.; Sparling, D. W.; Cowardin, L. M. (1987) A model of the productivity of the mallard duck. Ecol. Model. 38: 257-275.
- Johnson, M. A.; Hinz, T. C.; Kuck, T. L. (1988) Duck nest success and predators in North Dakota, South Dakota, and Montana: The Central Flyway Study. In: Uresk, D. W.; Schenbeck, G. L.; Cefkin, R., tech. coords. Eighth Great Plains wildlife damage control workshop proceedings; April 28-30, 1987; Rapid City, South Dakota. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; pp. 125-133.
- Jorde, D. G.; Krapu, G. L.; Crawford, R. D. (1983) Feeding ecology of mallards wintering in Nebraska. J. Wildl. Manage. 47: 1044-1053.
- Kantrud, H. A.; Stewart, R. E. (1977) Use of natural basin wetlands by breeding waterfowl in North Dakota. J. Wildl. Manage. 41: 243-253.
- Kirby, R. E.; Cowardin, L. M. (1986) Spring and summer survival of female mallards from northcentral Minnesota. J. Wildl. Manage. 50: 38-43.
- Kirby, R. E.; Riechmann, J. H.; Cowardin, L. M. (1985) Home range and habitat use of forest-dwelling mallards in Minnesota. Wilson Bull. 97: 215-219.
- Klett, A. T.; Johnson, D. H. (1982) Variability in nest survival rates and implications to nesting studies. Auk 99: 77-81.
- Klett, A. T.; Shaffer, T. L.; Johnson, D. H. (1988) Duck nest success in the prairie pothole region. J. Wildl. Manage. 52: 431-440.
- Krapu, G. L. (1981) The role of nutrient reserves in mallard reproduction. Auk 98: 29-38.
- Krapu, G. L.; Doty, H. A. (1979) Age-related aspects of mallard reproduction. Wildfowl 30: 35-39.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Lee, F. B.; Jessen, R. L.; Ordal, N. J.; et al. (1964) In: Moyle, J. B., ed. Ducks and land use in Minnesota. Minn. Dept. Conserv. Tech. Bull. 8.
- Lokemoen, J. T.; Schnaderbeck, R. W.; Woodward, R. O. (1988) Increasing waterfowl production on points and islands by reducing mammalian predation. In: Uresk, D. W.; Schenbeck, G. L.; Cefkin, R., tech. coord. Eighth Great Plains wildlife damage control workshop proceedings; April 28-30, 1987; Rapid City, South Dakota. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; pp. 146-148.

2-50 Mallard

- Lokemoen, J. T.; Duebbert, H. F.; Sharp, D. E. (1990a) Homing and reproductive habits of mallards, gadwalls, and blue-winged teal. Wildl. Monogr. 106: 1-28.
- Lokemoen, J. T.; Johnson, D. H.; Sharp, D. E. (1990b) Weights of wild mallard *Anas platyrhynchos*, gadwall *A. strepera*, and blue-winged teal *A. discors* during the breeding season. Wildfowl 41: 122-130.
- Martin, A. C.; Zim, H. S.; Nelson, A. L. (1951) American wildlife and plants. New York, NY: McGraw-Hill Book Company, Inc.
- McAtee, W. L. (1918) Food habits of the mallard ducks of the United States. U.S. Dept. Agric. Bull. 720.
- McEwan, E. H.; Koelink, A. F. (1973) The heat production of oiled mallards and scaup. Can. J. Zool. 51: 27-31.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Nelson, A. L.; Martin, A. C. (1953) Gamebird weights. J. Wildl. Manage. 17: 36-42.
- Palmer, R. S. (1976) Handbook of North American birds: v. 1. New Haven, CT: Yale University Press.
- Perret, N. G. (1962) The spring and summer foods of the common mallard (*Anas platyrhynchos platyrhynchos* L.) in south central Manitoba [master's thesis]. Vancouver, BC: University of British Columbia.
- Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.
- Pospahala, R. S.; Anderson, D. R.; Henny, C. J. (1974) Breeding habitat conditions, size of the breeding populations, and production indices in population ecology of the mallard. Bureau of Sport Fish. and Wildl., Res. Publ. 115, U.S. GPO Stock No. 2410-00387.
- Ringelman, J. K.; Eddleman, W. R.; Miller, H. W. (1989) High plains reservoirs and sloughs. In: Smith, L. M.; Pederson, R. L.; Kaminski, R. M., eds. Habitat management for wintering waterfowl in North America. Lubbock, TX: Texas Tech University Press; pp. 311-340.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.

2-51 Mallard

- Rutherford, W. H. (1966) Chronology of waterfowl migration in Colorado. Colo. Div. Wildl.; Game Inf. Leafl. No. 42.
- Simpson, S. G. (1988) Duck nest success on South Dakota game production areas. In:
 Uresk, D. W.; Schenbeck, G. L.; Cefkin, R., tech. coords. Eighth Great Plains wildlife
 damage control workshop proceedings; April 28-30, 1987; Rapid City, South Dakota.
 Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain
 Forest and Range Experiment Station; pp. 140-145.
- Stoudt, J. H. (1944) Food preferences of mallards on the Chippewa National Forest, Minnesota. J. Wildl. Manage 8: 100-112.
- Swanson, G. A.; Meyer, M. I. (1973) The role of invertebrates in the feeding ecology of Anatinae during the breeding season. In: The Waterfowl Habitat Management Symposium at Moncton, New Brunswick, Canada; July 30 August 1, 1973; The Atlantic Waterfowl Council; pp. 143-180.
- Swanson, G. A.; Krapu, G. L.; Serie, J. R. (1979) Foods of laying female dabbling ducks on the breeding grounds. In: Bookhout, T. A., ed. Waterfowl and wetlands--an integrated review: proceedings of 1977 symposium. Madison, WI: The Wildlife Society, NC Sect.; pp. 47-57.
- Swanson, G. A.; Meyer, M. I.; Adomaitis, V.A. (1985) Foods consumed by breeding mallards on wetlands of south-central North Dakota. J. Wildl. Manage. 49: 197-203.
- Toft, C. A.; Trauger, D. L.; Murdy, H. W. (1984) Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Athya*, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53: 75-92.
- USFWS. (1991) 1991 Status of waterfowl & fall flight forecast. Laurel, MD: U.S. Fish Wildl. Serv., Office of Migratory Bird Management.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Whyte, R. J.; Bolen, E. G. (1984) Impact of winter stress on mallard body composition. Condor 86: 477-482.

2-52 Mallard

2.1.4. Lesser Scaup (bay ducks)

Order Anseriformes, Family Anatidae. Bay ducks are adapted for diving and characteristically need a running start to become airborne because their legs are located further back on their body than on other ducks. They breed at mid to high latitudes and winter in flocks on large water bodies and in protected coastal bays and river mouths. Bay ducks dive for their food, and their diet is omnivorous (i.e., both plant and animal matter) and depends on the seasonal and regional abundance of food resources. Because of their food habits, bay ducks prefer deeper, more permanent ponds than dabbling ducks (Bellrose, 1976). The sexes vary in coloration, and different bay duck species range in length from 42 to 53 cm (bill tip to tail tip).

Selected species

The lesser scaup (*Aythya affinis*) is one of the most abundant North American ducks (Allen, 1986). They breed principally throughout western Canada and Alaska, although their breeding range extends into the western United States as far south as Colorado and Ohio. Lesser scaup winter in the United States in the Mississippi flyway and the Atlantic flyway (Bellrose, 1976). They also winter along all coastal areas in the southern states and into Mexico (National Geographic Society, 1987).

Body size. The lesser scaup averages 42 cm from bill tip to tail tip. Males are larger and more colorful than the brown females (Bellrose, 1976; see table). Following their postbreeding molt, scaups increase their fat reserves in preparation for migration (Austin and Fredrickson, 1987; see table).

Habitat. Lesser scaup are found on large lakes and bays during the fall and winter and are common on smaller bodies of water (e.g., ponds) during the spring. They breed in the prairie potholes region, most often on permanent or semipermanent wetlands of 0.85 to 2.0 ha with trees and shrubs bordering at least half of the shorelines (Bellrose, 1976; Smith, 1971, cited in Allen, 1986). Primary brood habitat is characterized by permanent wetlands dominated by emergent vegetation (Smith, 1971, cited in Allen, 1986). In a study of ducks wintering in South Carolina, Bergan and Smith (1989) found lesser scaup would forage primarily in areas with submergent vegetation but also in areas of emergent vegetation, shallow open water, and floating-leaved vegetation. They found some differences in foraging habitat use by season and between males and females. In particular, females tended to use more shallow habitats than males, and males preferred open water in late fall (Bergan and Smith, 1989).

Food habits. Most populations of lesser scaup consume primarily aquatic invertebrates, both from the water column and from the surfaces of aquatic vegetation and other substrates (Tome and Wrubleski, 1988; Bartonek and Hickey, 1969). Common prey include snails, clams, scuds (amphipods), midges, chironomids, and leeches (see table). Scaup are omnivorous, however, and the percentage of plant materials (almost exclusively seeds) in the diet varies seasonally as the availability of different foods changes (Afton et al., 1991; Dirschl, 1969; Rogers and Korschgen, 1966). When seeds are locally abundant, they may be consumed in large quantities (Dirschl, 1969). Breeding females and ducklings

eat mostly aquatic invertebrates (Sugden, 1973). Young ducklings feed primarily on water-column invertebrates (e.g., phantom midges, clam shrimps, water mites), whereas older ducklings forage mainly on bottom-dwelling invertebrates (e.g., scuds or amphipods, dragonflies, caddisflies) (Bartonek and Murdy, 1970). During the winter, there are no significant differences in diet between juveniles and adults or between males and females (Afton et al., 1991).

Molt. Nonbreeding and postbreeding males and nonbreeding females generally leave the breeding grounds in June to molt on lakes. However, some males complete their molt on the breeding grounds (Trauger, 1971, cited in Bellrose, 1976). Large flocks of molting birds become flightless during the wing molt phase, which begins in July and is usually complete by late August (McKnight and Buss, 1962).

Migration. The axis of the main migration corridor extends from the breeding grounds on the Yukon Flats, Alaska, to wintering areas in Florida (Bellrose, 1976). Most scaup winter in the United States, with the greatest numbers in the Mississippi flyway and the Atlantic flyway. They start to arrive at their wintering areas in mid-October (Bellrose, 1976). The timing of northward migration in the spring varies from February to May (Bellrose, 1976). Before migration, scaup gain weight by increasing their body fat content (Austin and Fredrickson, 1987).

Breeding activities and social organization. Scaup build nests on the ground among tall grasses, shrubs, or forbs where plant heights range from 20 to 60 cm (Hines, 1977). Nests can be located along the edge of shorelines to upland areas (Bellrose, 1976). Courtship and pair bonds start to form on the wintering grounds, and pairs typically remain together for only one season. Males do not remain long after incubation commences (Trauger, 1971, cited in Bellrose, 1976). The female and her brood leave the vicinity of the nest shortly after the ducklings have hatched. Most broods are on their own by 4 to 5 weeks of age (Gehrman, 1951, cited in Bellrose, 1976) and fledge between 7 and 9 weeks of age (Bellrose, 1976; Lightbody and Ankney, 1984). Females of this species often lay eggs in other lesser scaup nests (nest parasitism), which can result in large compound clutches of lesser scaup eggs in a single nest (Hines, 1977). Hines (1977) also found that mixing of broods was common in Saskatchewan; by August, groups of 15 to 40 ducklings led by two to three hens would be common. Female lesser scaup also occasionally lay eggs in the nests of other ducks (e.g., gadwall; Hines, 1977).

Home range and resources. Relatively small nesting territories and large highly overlapping foraging ranges are characteristic of lesser scaup (Hammel, 1973, cited in Allen, 1986). Several pairs can nest in close proximity without aggression, each defending only a small area immediately surrounding the nest (Bellrose, 1976; Vermeer, 1970). In Manitoba, Hammel (1973) estimated the mean minimum foraging home range to be 89 ± 6.5 ha. Initial areas occupied by pairs usually contain stumps, logs, boulders, or beaches as loafing sites, but later lesser scaup rely solely on open water (Gehrman, 1951, cited in Bellrose, 1976).

Population density. In winter, local densities of scaup can be very high, as large flocks float on favored feeding areas (Bellrose, 1976). In summer, the density of breeding

pairs increases with the permanence and size of the ponds (Kantrud and Stewart, 1977; see table).

Population dynamics. In some populations, many yearling and some 2-year-olds do not breed; the proportion breeding tends to increase with improving water and habitat conditions (Afton, 1984; McKnight and Buss, 1962). In a 4-year study in Manitoba, Afton (1984) found that, on average, 30 percent of 1-year-olds and 10 percent of 2-year-olds, did not breed. Clutch size and reproductive performance of adult females generally increase with age (Afton, 1984). Most nest failures are due to predation (e.g., by mink, raccoons, red fox), and scaup often attempt to renest if the initial nest fails (Afton, 1984; Bellrose, 1976). Annual mortality for juveniles is higher than that for adults, and adult female mortality exceeds adult male mortality (Smith, 1963; see table).

Similar species (from general references)

- The redhead (Aythya americana), a larger bay duck (48 cm), breeds on lakes and ponds in the northwestern United States and in midwestern Canada. They winter in coastal areas and the southern United States and Mexico. In summer, adult female and juvenile redheads consume predominantly animal matter (e.g., caddis flies, midges, water fleas, snails), while males include more plant materials in their diet.
- The canvasback (*Aythya valisineria*) is the largest bay duck (53 cm). They are common on lakes and ponds in the northern United States and southern Canada during the breeding season and along coastal areas of the United States during winter. Studies during the winter in North and South Carolina have found varying diets for canvasbacks, consuming mostly animal matter (e.g., clams); others eat only vegetation. In summer, adult female and juvenile canvasbacks eat predominantly animal material (e.g., caddis flies, snails, mayflies, midges), whereas adult males may eat predominantly vegetable material, particularly tubers of *Potamogeton*.
- The ring-necked duck (*Aythya collaris*) is similar in size (43 cm) to the lesser scaup and prefers freshwater wetlands. They are commonly seen on woodland lakes and ponds, but in winter also use southern coastal marshes. During the winter, ring-necked ducks eat mostly plant materials (81 percent) and a variety of animal matter (19 percent).
- The greater scaup (*Aythya marila*) (46 cm) is common in coastal areas and the Great Lakes during winter. They are omnivorous, eating 50 to 99 percent animal matter and the remainder plant foods during the winter.

General references

Allen (1986); Bartonek and Hickey (1969); Bellrose (1976); National Geographic Society (1987); Perry and Uhler (1982).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	F preflightless F flightless F postflightless F migratory	688 647 693 842		Manitoba, Canada	Austin & Fredrickson, 1987	1
	F M	770 860	up to 950 up to 1,100	United States	Nelson & Martin, 1953	
Adult Body Fat (grams lipid: % of total body weight)	F preflightless F flightless F postflightless F migratory	50.7 (7.4%) 37.2 (5.7%) 46.5 (6.7%) 188.1 (22.3%)		Manitoba, Canada	Austin & Fredrickson, 1987	1
Duckling Growth Rate	age in weeks 0-3 3-6 6-9 9-12	growth in g/day 6.9 14 1.5	(final body weight) (190 g) (485 g) (516 g) (542 g)	Utah or Canada	Sugden & Harris, 1972	2
Metabolic Rate (kcal/kg-day)	A F basal A M basal A B resting	83 81 90		Canada	estimated McEwan & Koelink, 1973	3
	20 to 30°C A F free-living A M free-living	216 211	(102 - 457) (99 - 445)	Canada	estimated	4
Food Ingestion Rate (g/g-day)	juveniles, both sexes: 1 - 5 weeks 6 - 12 weeks	dry matter intake/ wet body weight 0.162 0.077		Saskatchewan/captive: reared in large brooder and in outdoor pens	Sugden & Harris, 1972	5
Water Ingestion Rate (g/g-day)	A F A M	0.064 0.062			estimated	6
Inhalation Rate (m³/day)	A F A M	0.34 0.36			estimated	7

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Lesser Scaup

Lesser Scaup (Aythya affinis)

Factors	Age/Se Cond./S		Mean		Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Surface Area (cm²)	A F A M		842 906				estimated	8
Dietary Composition		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
(animal) midges snails grass shrimp (plant - seeds) bulrush (plant - vegetativ green algae	re)				(60.9) 45.9 7.7 7.3 (36.1) 36.0 (3.0) 2.3	Louisiana/lakes, marshes (% dry weight; esophageal & proventricular contents)	Afton et al., 1991	
juveniles only: (animal) scuds phantom midge clam shrimps dragon/damseli water bugs water mites caddis flies water beetles mayflies (plants)			(100) 1 ± 1 54 ± 8 30 ± 8 - 4 ± 3 8 ± 3 - 1 ± 1 2 ± 1 (trace)	(100) 57 ± 1 2 ± 2 17 ± 1 11 ± 1 6 ± 5 4 ± 3	9 B 7	Northwest Territories/lake (% wet volume ± SE; esophageal contents)	Bartonek & Murdy, 1970	

Lesser Scaup (Aythya affinis)

Dietary						Location/Habitat		Note
Composition		Spring	Summer	Fall	Winter	(measure)	Reference	No.
adults only:						nw Minnesota: spring and fall	Afton et al., 1991	
(animal)		(91.8)		(90.5)		migrations/lakes, marshes,	Alton et al., 1991	
scuds (amphipe	nde)	33.2		54.9		pools		
dragonflies	ous,	33.2		2.4		pools		
caddis flies		8.8		7.6		(% dry weight;		
midges		2.3		7.0		esophageal & proventricular		
other insects		4.9		_		contents)		
snails		31.9		10.2		Contents)		
fingernail clams	2	6.0		5.1				
brook stickleba		- 0.0		4.1				
fathead minnov		_		5.0				
other fish	•	3.5		3.0				
(plants - seeds)		(6.0)		(9.4)				
(plants - vegetati	ve)	(2.2)		(0.1)				
(pianie regenan	,	(=:=)		(011)				
(animal)		(90.9)	(75.1)	(49.6)		Saskatchewan,	Dirschl, 1969	
scuds		66.0	9.8	42.5		Canada/shallow lakes		
diptera		-	1.3	0.1				
leeches		12.0	23.7	1.6		(% dry weight; esophagus		
fingernail clams	3	12.7	25.7	-		and proventriculus contents)		
cyprinid fish		-	2.9	-				
caddis flies		0.2	1.6	1.9				
clam shrimps		-	3.1	0.5				
(plant - seeds)		(9.1)	(24.9)	(50.4)				
Nuphar variega	tum	-	13.2	42.8				
other seeds		9.1	11.7	7.6				
B	A 'O							N
Population	Age/S		84			Lagadian Alabitat	Defenses	Note
Dynamics	Cond.	/Seas.	Mean	Ra	inge	Location/Habitat	Reference	No.
Home Range	breed	lina	89 ± 6.5 SE			Manitoba, Canada	Hammel, 1973	9
Size (ha)						,		

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (pairs/ha)	A B seasonal wetland A B permanent	0.029		North Dakota/ prairie potholes	Kantrud & Stewart, 1977	
	wetland A B island in lake	0.061 28.9	13.1 - 58.5	Alberta, Canada/islands in lakes of parklands and boreal forest	Vermeer, 1970	10
Clutch		9.47 ± 0.18 SE	7 - 12	Saskatchewan/marsh island	Hines, 1977	
Size	2nd yr female 4th yr female	10.0 ± 0.2 SE 12.1 ± 0.2 SE	8 - 12 11 - 14	Manitoba/lake	Afton, 1984	
Clutches /Year		1, but often renest if lost		NS/NS	Afton, 1984	
Days Incubation		24.8	21 - 27	NS/NS	Vermeer, 1968	10
Age at Fledging (days)	В	65 ± 0.91 SE		Manitoba/captive	Lightbody & Ankney, 1984	
Percent Nests Hatching	1st yr female 2nd yr female 3rd yr female	26.3 22.2 45.5		Manitoba/lake	Afton, 1984	
		76		Saskatchewan/marsh islands	Hines, 1977	
Percent Broods Surviving	up to 20 days of age	67.5 ± 4.9 SE		Manitoba/lake	Afton, 1984	
Age at First Breeding	M F	most in 2nd yr 1 - 2 years		NS/NS Manitoba/lake	Palmer, 1976 Palmer, 1976; Afton, 1984	
Annual Mortality Rates (percent)	juveniles A males A females	68 - 71 38 - 52 49 - 60		NS/NS	Smith, 1963	

Lesser Scaup (Aythya affinis)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	early June early May	early June	early July	Manitoba, Canada Montana	Afton, 1984 Ellig, 1955	10
Hatching	early July	mid-July	early August	NW Territory and Saskatchewan, Canada	Toft et al., 1984; Hines, 1977	
Molt (fall)	July		September	Manitoba, Canada	Austin & Fredrickson, 1987	
Migration spring	early February mid-April	March - April	Мау	departing United States arriving Manitoba, Canada	Bellrose, 1976 Afton, 1984	
fall	September		mid-November	Pacific flyway (s OR, n CA)	Gammonley & Heitmeyer, 1990 Bellrose, 1976	
	mid-October	mid- November	December	arriving United States	Benrose, 1970	

- 1 Four stages of feather molt evaluated.
- 2 Ducklings stopped growing at rate typical of wild birds around 6 weeks of age. By 12 weeks, they weighed approximately 200 g less than typical of wild scaup.
- 3 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Nelson and Martin (1953).
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Nelson and Martin (1953).
- 5 Young ducklings maintained in 18 to 27 °C brooder, then in outdoor pens with same temperature range. Metabolizable energy of amphipods (estimated to be 3.11 kcal/g dry wt), a typical scaup food, is similar to the commercial diet used in the experiment (3.09 kcal/g dry wt). Ducklings stopped growing as rapidly as would wild ducklings at about 6 weeks of age. For methods of estimating food ingestion rates for adult scaup, see Chapters 3 and 4.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Nelson and Martin (1953).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Nelson and Martin (1953).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from Nelson and Martin (1953).
- 9 Relatively small, highly overlapping, home ranges. Cited in Allen (1986).
- 10 Cited in Bellrose (1976).

References (including Appendix)

- Afton, A. D. (1984) Influence of age and time on reproductive performance of female lesser scaup. Auk 101: 255-265.
- Afton, A. D.; Hier, R. H.; Paulus, S. L. (1991) Lesser scaup diets during migration and winter in the Mississippi flyway. Can. J. Zool. 69: 328-333.
- Allen, A. W. (1986) Habitat suitability index models: lesser scaup. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.117).
- Austin, J. E.; Fredrickson, L. H. (1987) Body and organ mass and body composition of postbreeding female lesser scaup. Auk 104: 694-699.
- Bartonek, J. C.; Hickey, J. J. (1969) Food habits of canvasbacks, redheads, and lesser scaup in Manitoba. Condor 71: 280-290.
- Bartonek, J. C.; Murdy, H. W. (1970) Summer foods of lesser scaup in subarctic taiga. Arctic 23: 35-44.
- Bellrose, F. C. (1976) Ducks, geese, and swans of North America. Harrisburg, PA: The Stackpole Co.
- Bergan, J. F.; Smith, L. M. (1989) Differential habitat use by diving ducks wintering in South Carolina. J. Wildl. Manage. 53: 1117-1126.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Chabreck, R. H.; Takagi, T. (1985) Foods of lesser scaup in crayfish impoundments in Louisiana. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 39: 465-470.
- Chappel, W. A.; Titman, R. D. (1983) Estimating reserve lipids in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*). Can. J. Zool. 61: 35-38.
- Dirschl, H. J. (1969) Foods of lesser scaup and blue-winged teal in the Saskatchewan River Delta. J. Wildl. Manage. 33: 77-87.
- Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.
- Ellig, L. J. (1955) Waterfowl relationships to Greenfields Lake, Teton County, Montana.

 Mont. Fish. and Game Comm. Tech. Bull. 1.
- Gammonley, J. H.; Heitmeyer, M. E. (1990) Behavior, body condition, and foods of buffleheads and lesser scaups during spring migration through the Klamath Basin, California. Wilson Bull. 102: 672-683.

- Gehrman, K. H. (1951) An ecological study of the lesser scaup duck (*Athaya affinis Eyton*) at West Medical Lake, Spokane County, Washington [master's thesis]. Pullman, WA: Washington State College.
- Gollop, J. B.; Marshall, W. H. (1954) A guide for aging duck broods in the field (mimeo). MS: Mississippi Flyway Council Tech. Sect.
- Hammel, G. S. (1973) The ecology of the lesser scaup (*Athaya affinis* Eyton) in southwestern Manitoba [master's thesis]. Guelph, Ontario: University of Guelph.
- Hines, J. E. (1977) Nesting and brood ecology of lesser scaup at Waterhen Marsh, Saskatchewan. Can. Field-Nat. 91: 248-255.
- Hoppe, R. T.; Smith, L. M.; Wester, D. B. (1986) Foods of wintering diving ducks in South Carolina. J. Field Ornithol. 57: 126-134.
- Hunt, E. G.; Anderson, W. (1966) Renesting of ducks at Mountain Meadows, Lassen County, California. Calif. Fish and Game 52: 17-27.
- Kantrud, H. A.; Stewart, R. E. (1977) Use of natural basin wetlands by breeding waterfowl in North Dakota. J. Wildl. Manage. 41: 243-253.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Lightbody, J. P.; Ankney, C. D. (1984) Seasonal influence on the strategies of growth and development of canvasback and lesser scaup ducklings. Auk 101: 121-133.
- McEwan, E. H.; Koelink, A. F. (1973) The heat production of oiled mallards and scaup. Can. J. Zool. 51: 27-31.
- McKnight, D. E.; Buss, I. O. (1962) Evidence of breeding in yearling female lesser scaup. J. Wildl. Manage. 26: 328-329.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- Nasser, J. R. (1982) Management of impoundments for crayfish and waterfowl [master's thesis]. Baton Rouge, LA: Louisiana State University.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.

- Nelson, A. L.; Martin, A. C. (1953) Gamebird weights. J. Wildl. Manage. 17: 36-42.
- Palmer, R. S. (1976) Handbook of North American birds: v. 2, 3. New Haven, CT: Yale University Press.
- Perry, M. C.; Uhler, F. M. (1982) Food habits of diving ducks in the Carolinas. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 36: 492-504.
- Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.
- Rienecker, W. C.; Anderson, W. (1960) A waterfowl nesting study on Tule Lake and Lower Klamath National Wildlife Refuges, 1957. Calif. Fish and Game 46: 481-506.
- Ringelman, J. K.; Eddleman, W. R.; Miller, H. W. (1989) High plains reservoirs and sloughs. In: Smith, L. M.; Pederson, R. L.; Kaminski, R. M., eds. Habitat management for wintering waterfowl in North America. Lubbock, TX: Texas Tech University Press; pp. 311-340.
- Rogers, J. P. (1962) The ecological effects of drought on reproduction of the lesser scaup, *Aythya affinis* (Eyton) [Ph.D. dissertation]. Columbia, MO: University of Missouri.
- Rogers, J. P.; Korschgen, L. J. (1966) Foods of lesser scaups on breeding, migration, and wintering areas. J. Wildl. Manage. 30: 258-264.
- Rowinski, L. J. (1958) A review of waterfowl investigations and a comparison of aerial and ground censusing of waterfowl at Minto Flats, Alaska. Mimeogr. Rep.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Rutherford, W. H. (1966) Chronology of waterfowl migration in Colorado. Colo. Div. Wildl.; Game Inf. Leafl. No. 42.
- Siegfried, W. R. (1974) Time budget of behavior among lesser scaups on Delta Marsh. J. Wildl. Manage. 38: 708-713.
- Smith, A. G. (1971) Ecological factors affecting waterfowl production in Alberta parklands. U.S. Fish Wildl. Serv. Resour. Publ. 92.
- Smith, R. I. (1963) Lesser scaup and ring-necked duck shooting pressure and mortality rates. Bur. Sport Fish & Wildl. Adm. Rep. 20.
- Sugden, L. G. (1973) Feeding ecology of pintail, gadwall, American widgeon and lesser scaup ducklings in Southern Alberta. Can. Wildl. Serv. Rep. Ser. No. 24.
- Sugden, L. G.; Harris, L. E. (1972) Energy requirements and growth of captive lesser scaup. Poultry Sci. 51: 625-633.

- Swanson, G. A.; Krapu, G. L.; Bartonek, J. C.; et al. (1974) Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38: 302-307.
- Toft, C. A.; Trauger, D. L.; Murdy, H. W. (1984) Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Athya*, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53: 75-92.
- Tome, M. W.; Wrubleski, D. A. (1988) Underwater foraging behavior of canvasbacks, lesser scaups, and ruddy ducks. Condor 90: 168-172.
- Townsend, G. H. (1966) A study of waterfowl nesting on the Saskatchewan River delta. Can. Field. Nat. 80: 74-88.
- Trauger, D. L. (1971) Population ecology of lesser scaup (*Athaya affinis*) in subarctic taiga [Ph.D. dissertation]. Ames, IA: Iowa State University.
- Vermeer, K. (1968) Ecological aspects of ducks nesting in high densities among larids. Wilson Bull. 80: 78-83.
- Vermeer, K. (1970) Some aspects of the nesting of ducks on islands in Lake Newell, Alberta. J. Wildl. Manage. 34: 126-129.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

2.1.5. Osprey (Pandion haliaetus)

Order Falconiformes, Family Accipitridae. The only North American member of the subfamily Pandioninae, these large birds of prey have long narrow wings, a sharp hooked bill, and powerful talons. Osprey are found near freshwater or saltwater, and their diet is almost completely restricted to fish. They are adapted for hovering over the water and dive feet-first, seizing fish with their talons (Robbins et al., 1983). Once very rare owing to DDT accumulation in their food (1950's to early 1970's), osprey now are increasing in numbers. In the United States, there are five regional populations of osprey (in order of abundance): Atlantic coast, Florida and gulf coast, Pacific Northwest, western interior, and Great Lakes (Henny, 1983). In North America, osprey breed primarily in a wide band from coast to coast across Canada and the southern half of Alaska, where they are not restricted to coastal and Great Lake areas as they are in the United States. However, osprey are reported from all States during the fall and spring migrations (Henny, 1986).

Body size. The various subspecies of osprey around the world differ in size, and in general females are heavier than males (Poole, 1989a; see table). Osprey found in the United States are considered to be of the subspecies *carolinenesis* and average 56 cm from bill tip to tail tip (Robbins et al., 1983) and weigh between 1.2 and 1.9 kg (see table).

Habitat. In the United States, the majority of osprey populations are associated with marine environments, but large inland rivers, lakes, and reservoirs also may support osprey (Henny, 1986, 1988b). Good nesting sites in proximity to open, shallow water and a plentiful supply of fish are the primary resources required for osprey success (Poole, 1989a). The tops of isolated and often dead trees and man-made structures are preferred nesting sites. Osprey often nest in colonies (Poole, 1989a).

Food habits. Osprey are almost completely piscivorous, although they have been observed on occasion taking other prey including birds, frogs, and crustaceans (Brown and Amadon, 1968). Their prey preferences change seasonally with the abundance of the local fish (Edwards, 1988; Greene et al., 1983). Osprey occasionally will pick up dead fish but only if fresh (Bent, 1937). Osprey are most successful catching species of slow-moving fish that eat benthic organisms in shallow waters and fish that remain near the water's surface (Poole, 1989a). Osprey consume all parts of a fish except the larger bones; later, bones and other undigestible parts are ejected in fecal pellets (Bent, 1937).

Molt. Juvenile plumage is fully developed by fledging at about 60 days of age (Henny, 1988b). Juveniles undergo a gradual molt to adult plumage at approximately 18 months of age (Brown and Amadon, 1968). For adults, the basic molt takes place in two phases; the first phase occurs primarily on the wintering grounds prior to spring migration. Completion of the molt occurs in the summer range prior to fall migration (Henny, 1988b).

Migration. Osprey are year-round residents in the most southern parts of their range (e.g., south Florida, Mexico) but are migratory over the rest of their range in the United States and Canada (Poole, 1989a). Studies of banded osprey have shown that the fall migration begins in late August in the north temperate zone, with adults and juveniles

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from the eastern and central United States comprising a broad front flying south and then directly across open ocean to their wintering grounds in Central and South America (Poole, 1989a). Spring migration appears to follow the same routes with birds reaching, for example, the Chesapeake Bay area in mid-March (Reese, 1977) and Minnesota by the first half of April (Dunstan, 1973; Henny and Van Velzen, 1972). The majority of migrating osprey appear to follow the coastline, perhaps because they come from coastal colonies or because the coast offers abundant food (Poole, 1989a). After their first migration south, juveniles remain in their wintering grounds for about a year and a half, returning north to the breeding grounds as 2-year-olds (Henny and Van Velzen, 1972).

Breeding activities and social organization. Nonmigratory (i.e., year-round resident) populations breed during the winter; whereas migratory populations breed during the summer (Poole, 1989a). Monogamy is the general rule for osprey; breeding pairs remain together and return to the same nest site year after year (Fernandez and Fernandez, 1977; Henny, 1988b). Colonies of osprey occur in areas such as islands, reservoirs, or lakes that offer secure nesting sites and abundant food (Henny, 1986), but most osprey are solitary nesters, often separated from other nests by tens to hundreds of kilometers (Poole, 1989a). The female performs most of the incubation and relies completely on the male for food from just after mating until the young have fledged (Poole, 1989a). Van Daele and Van Daele (1982) found that ospreys at successful nests incubated 99.5 to 100 percent of the daylight hours; disturbance of the nest during this time can kill the eggs if the adults are kept from returning to the nest for some time. After hatching, the female is in constant attendance at the nest for the first 35 days but may perch nearby at intervals after that (Henny, 1988b). The female distributes the food delivered by the male by biting off pieces to feed to the young (Poole, 1989a). By 30 days, the nestlings have reached 70 to 80 percent of their adult weight and begin to be active in the nest (Poole, 1989a). The young fledge by age 60 to 65 days in nonmigratory populations and by about 50 to 55 days in migratory populations (Henny et al., 1991). After fledging, the young remain dependent on both parents for food usually for an additional 2 to 3 weeks (Poole, 1989a), but dependency can continue up to 6 weeks in the more southern populations (Henny, 1986).

Home range and resources. Osprey build large stick nests in the tops of tall trees or artificial structures such as buoys and radio towers (Poole, 1989a). In the Chesapeake Bay area, less than one third of the 1,450 breeding pairs built their nests in trees, while over half nested on channel markers and duck blinds, and the remainder on miscellaneous man-made structures (Henny et al., 1974). Osprey build their nest at the top of the chosen site, which can make it vulnerable to destruction from high winds (Henny, 1986). If not lost, the same nest often is used year after year, and it can become quite large (e.g., over 2 m tall and 1.5 m across) (Dunstan, 1973; Henny, 1988a). On islands where no predators are present, osprey will nest on the ground (Poole, 1989b). The distance osprey travel from their nests to forage (i.e., foraging radius) depends on the availability of appropriate nest sites near areas with sufficient fish; osprey will travel up to 10 to 15 km to obtain food (Van Daele and Van Daele, 1982).

Population density. Population density depends on the availability and distribution of resources and can be highly variable. Henny (1988a) reported as many as 1.9 nests per hectare in one of the largest osprey colonies in the western United States in 1899, with an

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estimated 1.0 to 1.2 nests per hectare occupied that year. Lower densities on the order of 0.005 to 0.1 nests per hectare are more common (see table).

Population dynamics. Breeding data from many locations in the United States and Canada during the years 1950 to 1976 show low productivity (fewer than one chick fledged per active nest on average). Evidence indicates the cause to be egg-shell thinning that resulted from the ospreys' exposure to DDT that had bioaccumulated in fish (Henny and Anthony, 1989; Henny et al., 1977; Poole, 1989a). Thus, data from reproductive studies conducted during this time can only be used with this in mind (Spitzer et al., 1978).^a Because of their terminal position in the aquatic food chain, osprey can be a sensitive indicator of toxic contaminants that bioaccumulate (Henny et al., 1978; Henny, 1988b).

Osprey are only known to start a second clutch if the first one is destroyed (Poole, 1989a). Juveniles do not return to their place of birth until 2 years of age, and they do not breed until their third season (Henny and Van Velzen, 1972). Often, breeding is delayed until 4 to 7 years of age in areas such as the Chesapeake Bay, where good nesting sites are scarce (Poole, 1989b).

General references

Poole (1989a); Brown and Amadon (1968); Henny (1986); Henny (1988b).

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^aIn the table beginning on the next page, data on the number fledged per active nest and the number fledged per successful nest are provided only for studies of populations that appeared to be unaffected by DDT.

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A F A M	1,568 1,403	1,250 - 1,900 1,220 - 1,600	NS	Brown & Amadon, 1968	
	A F courtship A F incubation A F late nestl. A M courtship A M late nestl.	1,880 ± 20 SE 1,925 ± 25 SE 1,725 ± 25 SE 1,480 ± 15 SE 1,420 ± 15 SE		se Massachusetts	Poole, 1984	1
	F at fledging M at fledging	1,510 1,210		Maryland, Virginia	McLean, 1986	
Egg Weight (g)		72.2 ± 5.35 SD	66.0 - 81.3	North Carolina (carolinensis)	Whittemore, 1984	
Metabolic Rate (kcal/kg-day)	A F basal A M basal	69 71			estimated	2
	A F free-living A M free-living	181 186	(85 - 384) (87 - 395)		estimated	3
Food Ingestion Rate (g/g-day)	A F courtship period	0.21		se Massachusetts	Poole, 1983	
Water Ingest. Rate (g/g-day)	A F A M	0.051 0.053			estimated	4
Inhalation Rate (m³/day)	A F A M	0.578 0.531			estimated	5
Surface Area (cm²)	AF	1,353			estimated	6

Osprey (Pandion haliaetus)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
alewife smelt pollock winter flounder		32 5 53 10			Nova Scotia, Canada/ harbor, bay (% wet weight; observed captures)	Greene et al., 1983	7
starry flounder cutthroat trout		95 5			se Alaska/NS (% wet weight; observed captures, noting fish length)	Hughes, 1983	7
carp crappie		67 33			w Oregon/NS (% wet weight; observed captures, noting fish length)	Hughes, 1983	7
gizzard shad sunfish largemouth bass golden shiner	63 29 5 3				Florida/lake (% of prey caught; identified at nests)	Collopy, 1984	
brown bullhead salmonids northern squawfish yellow perch largescale sucker	37.7 20.8 19.3 11.6 10.6				ldaho/reservoir (% of fish caught; observed captures)	Van Daele & Van Daele, 1982	
Size of fish caught: < 10 cm 11 - 20 cm 21 - 30 cm 31 - 40 cm 41 + cm		3.3 42.1 46.7 6.6 1.3			Idaho/reservoir (% of fish in each size class; determined from remains at nest)	Van Daele & Van Daele, 1982	

Osprey (Pandion haliaetus)

Population Dynamics	Age/Sex Cond/Seas	Mean	Range	Location/Habitat	Reference	Note No.
Foraging Radius (km)	A M A B spring A B	1.7 10 3 to 8	0.7 - 2.7 > 1	Minnesota/lakes Nova Scotia/coastal nw California/coastal, bay	Dunstan, 1973 Greene et al., 1983 Koplin, 1981	
Population Density (nests/ha)	A B summer A B spring A B spring A B spring	1.9 0.028 0.10 0.005		Oregon/lake in 1899 only Florida/wetland North Carolina/reservoir North Carolina/lake	Henny, 1988a Eichholz, 1980 Henny & Noltemeier, 1975 Henny & Noltemeier, 1975	
Clutch Size		3.23 ± 0.03 SE 2.84 ± 0.07 SE 2.67 ± 0.07 SE 3.23 ± 0.09 SE 2.82	1 - 4	Atlantic Seaboard/NS Georgia, Florida/NS s California, n Mexico/NS ne United States/NS Idaho/river, lakes	Judge, 1983 Judge, 1983 Judge, 1983 Spitzer, 1980 Henny et al., 1991	
Clutches/Year		1		NS/NS	Poole, 1989a	8
Days Incubation		38.1 ± 3.2 SD	32 - 42	Baja California, Mexico/coastal islands	Judge, 1983	
			35 - 43	Massachusetts/NS	Poole, 1989a	
Age at Fledging (days)	non-migr. pop.	62.5 ± 4.9 SD	52 - 76	Baja California, Mexico/coastal islands	Judge, 1983	9
	migratory pop.	54 ± 3.0 SD	48 - 59	Maryland/Cheasapeake Bay	Stotts & Henny, 1975	9
Number Fledge per Active Nest		1.16 1.34 1.58 1.92	0.79 - 1.47 (10 yrs) 1.17 - 1.89 (3 yrs)	N. Carolina/lake S. Carolina/lake Idaho/reservoir e United States/coastal	Whittemore, 1984 Henny & Noltemeier, 1975 Van Daele & Van Daele, 1982 Poole, 1984	

Population Dynamics	Age/Sex Cond/Seas	Mean	Range	Location/Habitat	Reference	Note No.
Number Fledge per Successful		1.7		Baja California, Mexico/coastal islands	Judge, 1983	
Nest		2.14 1.83 1.79 2.05		Idaho/river Florida/lake Delaware/coastal bay Montana/lake	Henny et al., 1991 Collopy, 1984 Henny et al., 1977 Henny et al., 1991	
Age at Sexual Maturity	В В	3 yrs	3 - 5 yrs	New York, Massachusetts/NS North America/NS	Spitzer, 1980 Henny & Wight, 1969	10
Annual Mortality Rates (percent)	1st year years 2 - 18 J B A B	57.3 18.5 ± 1.8 41 15		New York, New Jersey/NS NS/NS	Henny & Wight, 1969 Spitzer, 1980	
Average Longevity	if reach sex. maturity	4.8		NS/NS	Brown & Amadon, 1968	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	late April early Dec. early January	May May	mid-June late February early March	Delaware, New Jersey Minnesota Florida (nonmigratory) Baja California, Mexico (nonmigratory)	Bent, 1937 Dunstan, 1973 Poole, 1989a Judge, 1983	
Hatching	mid-March late April February	early May mid-May	late May mid-June late April	Maryland, Virginia New York/New England Baja California, Mexico (nonmigratory)	Bent, 1937 Bent, 1937 Judge, 1983	
Migration fall	late August	September	November	most of United States	Henny, 1986	11
spring	early April early March			Minnesota North Carolina	Dunstan, 1973 Parnell & Walton, 1977	

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- 1 Late nestl. indicates late nestling stage of the breeding season. Cited in Poole (1989a).
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Brown and Amadon (1968).
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from Brown and Amadon (1968).
- 4 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Brown and Amadon (1968).
- 5 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Brown and Amadon (1968).
- 6 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from Brown and Amadon (1968).
- 7 Percent wet weight of food ingested by free-flying osprey estimated by identifying species of fish captured (using binoculars), estimating the length of each fish captured by comparison with osprey, and using laboratory measures of weights and lengths of samples of these fish species.
- 8 Second clutch produced only if first is lost.
- 9 Nestlings in migratory populations fledge at an earlier age than nestlings in nonmigratory populations, such as those in Mexico and south Florida.
- 10 Cited in Henny (1988b).
- 11 Cited in Henny (1986).

References (including Appendix)

- Bent, A. C. (1937) Life histories of North American birds of prey. Part 1: Order Falconiformes. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 167.
- Brown, L.; Amadon, D. (1968) Eagles, hawks, and falcons of the world, v. 1. New York, NY: McGraw-Hill.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Collopy, M. W. (1984) Parental care, productivity, and predator-prey relationships of ospreys in three North Florida Lakes: preliminary report. In: Westall, M. A., ed. Proc. southeastern U.S. and Caribbean osprey symposium; pp. 85-98.
- Cramp, S., chief ed. (1980) Handbook of the birds of Europe, the Middle East and North Africa: v. 2. Oxford, UK: Oxford University Press.
- Dunstan, T. C. (1968) Breeding success of osprey in Minnesota from 1963-1968. Loon 40: 109-112.
- Dunstan, T. C. (1973) The biology of ospreys in Minnesota. Loon 45: 108-113.
- Edwards, T. C., Jr. (1988) Temporal variation in prey preference patterns of adult ospreys. Auk 105: 244-251.
- Eichholz, N. F. (1980) Osprey nest concentrations in northwest Florida. Fla. Field Nat. 8: 18-19.
- Fernandez, G.; Fernandez, J. (1977) Some instant benefits and long range hopes of color banding ospreys. Transactions of the North American osprey research conference. U.S. Natl. Park Serv. Trans. Proc. Ser. 2.
- French, J. M. (1972) Distribution, abundance, and breeding status of ospreys in northwestern California [master's thesis]. Arcata, CA: Humboldt State University.
- French, J. M.; Koplin, J. R. (1977) Distribution, abundance, and breeding status of ospreys in northwestern California. Transactions of the North American osprey research conference, U.S. Natl. Park Serv. Trans. Proc. Ser. 2: 223-240.
- Garber, D. P. (1972) Osprey nesting ecology in Lassen and Plumas Counties, California [master's thesis]. Arcata, CA: Humboldt State University.

2-73 Osprey

- Greene, E. P.; Greene, A. E.; Freedman, B. (1983) Foraging behavior and prey selection by ospreys in coastal habitats in Nova Scotia, Canada. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 257-267.
- Grubb, T. C., Jr. (1977) Weather dependent foraging in ospreys. Auk 94: 146-149.
- Hagan, J. M. (1984) North Carolina osprey population: social group or breeding aggregation? In: Westall, M. A., ed. Proc. southeastern U.S. and Caribbean osprey symposium.
- Henny, C. J. (1977) Research, management and status of the osprey in North America. In: Chancellor, R. D., ed. Proc. world birds of prey conf. Internat. Council Bird Preserv.; Vienna, Austria; pp. 199-222.
- Henny, C. J. (1983) Distribution and abundance of nesting ospreys in the United States. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 175-186.
- Henny, C. J. (1986) Osprey (*Pandion haliaetus*), Section 4.3.1, US Army Corps of Engineers Wildlife Resources Management Manual. Prepared by U.S. Fish Wildl. Serv., Patuxent Wildl. Res. Center, Corvallis, OR for US Army Engineer Waterways Experiment Station, Vicksburg, MS: Technical Report EL-86-5.
- Henny, C. J. (1988a) Large osprey colony discovered in Oregon. Murrelet 69: 33-36.
- Henny, C. J. (1988b) Osprey [sections]. In: Palmer, R. S., ed. Handbook of North American birds: v. 4. New Haven, CT: Yale University Press.
- Henny, C. J.; Anthony, R. G. (1989) Bald eagle and osprey. Natl. Wildl. Fed. Sci. Tech. Ser. No. 12: 66-82.
- Henny, C. J.; Noltemeier, A. P. (1975) Osprey nesting populations in the coastal Carolinas. Amer. Birds 29: 1073-1079.
- Henny, C. J.; Van Velzen, W. T. (1972) Migration patterns and wintering localities of American ospreys. J. Wildl. Manage. 36: 1133-1141.
- Henny, C. J.; Wight, H. M. (1969) An endangered osprey population: estimates of mortality and production. Auk 86: 288-198.
- Henny, C. J.; Smith, M. M.; Stotts, V. D. (1974) The 1973 distribution and abundance of breeding ospreys in the Chesapeake Bay. Chesapeake Sci. 15: 125-133.
- Henny, C. J.; Byrd, M. A.; Jacobs, J. A.; et al. (1977) Mid-Atlantic coast osprey population: present numbers, productivity, pollutant contamination, and status. J. Wildl. Manage. 41: 254-265.

2-74 Osprey

- Henny, C. J.; Collins, J. A.; Deibert, W. J. (1978) Osprey distribution, abundance, and status in western North America. Murrlet 59: 14-25.
- Henny, C. J.; Blus, L. J.; Hoffman, D. J.; et al. (1991) Lead accumulation and osprey production near a mining site on the Coeur d'Alene River, Idaho. Arch. Environ. Contam. Toxicol. 21: 415-424.
- Hughes, J. (1983) On osprey habitat and productivity: a tale of two habitats. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 269-273.
- Judge, D. S. (1983) Productivity of ospreys in the gulf of California. Wilson Bull. 95: 243-255.
- Kennedy, R. S. (1973) Notes on the migration of juvenile ospreys from Maryland and Virginia. Bird-Banding 44: 180-186.
- Koplin, J. R. (1981) Reproductive performance of ospreys (*Pandion haliaetus*) in northwestern California. Natl. Geogr. Soc. Res. Rep. 13: 337-344.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Lind, G. S. (1976) Production, nest site selection, and food habits of ospreys in Deschutes National Forest, Oregon [master's thesis]. Corvallis, OR: Oregon State University.
- MacCarter, D. S. (1972) Food habits of osprey at Flathead Lake, Montana [master's thesis].

 Arcata, CA: Humboldt State University.
- MacNamara, M. (1977) Sexing the American osprey using secondary sexual characteristics. Transactions of the North American osprey research conference. U.S. Natl. Park Serv. Trans. Proc. Ser. 2: 43-45.
- McLean, P. K. (1986) The feeding ecology of Chesapeake Bay ospreys and the growth and behavior of their young [master's thesis]. Williamsburg, VA: College of William and Mary.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Melquist, W. E.; Johnson, D. R.; Carrier, W. D. (1978) Migration patterns of northern Idaho and eastern Washington ospreys. Bird-Banding 49: 234-236.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

2-75 Osprey

- Nesbitt, S. (1974) Foods of the osprey at Newnans Lake. Fla. Field Nat. 2: 45.
- Ogden, J. C. (1977) Preliminary report on a study of Florida ospreys. In: Ogden, J. C., ed. Transactions of the North American osprey research conference; pp. 143-151.
- Parnell, J. F.; Walton, R. (1977) Osprey reproductive success in southeastern North Carolina. Transactions North American osprey research conference. U.S. Natl. Park Serv. Trans. Proc. Ser. 2: 139-142.
- Peakall, D. B. (1988) Known effects of pollutants on fish-eating birds in the Great Lakes of North America. In: Toxic contamination in large lakes; v. 1; pp. 39-54.
- Poole, A. F. (1982) Brood reduction in temperate and subtropical ospreys. Oecologia (Berl.) 53: 111-119.
- Poole, A. F. (1984) Reproductive limitation in coastal ospreys: an ecological and evolutionary perspective [Ph.D. dissertation]. Boston, MA: Boston University.
- Poole, A. F. (1983) Courtship feeding, clutch size, and egg size in ospreys: a preliminary report. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 243-256.
- Poole, A. F. (1989a) Ospreys: a natural and unnatural history. Cambridge, MA: Cambridge University Press.
- Poole, A. F. (1989b) Regulation of osprey *Pandion haliaetus* populations: the role of nest side availability. In: Meyburg, B.-U.; Chancellor, R. D., eds. Raptors in the modern world: proceedings of the 3rd world conference on birds of prey and owls; 22-27 March 1987; Eilat, Israel. Berlin, London, Paris: World Working Group on Birds of Prey and Owls; pp. 227-234.
- Prevost, Y. A. (1977) Feeding ecology of ospreys in Antigonish County, Nova Scotia [master's thesis]. Montreal, Quebec: MacDonald College of McGill University.
- Prevost, Y. A. (1982) The wintering ecology of ospreys in Senegambia [Ph.D. dissertation]. Edinburgh, Scotland: University of Edinburgh.
- Prevost, Y. A.; Bancroft, R. P.; Seymour, N. R. (1978) Status of the osprey in Antigonish County, Nova Scotia. Can. Field-Nat. 92: 294-297.
- Reese, J. G. (1977) Reproductive success of ospreys in central Chesapeake Bay. Auk 94: 202-221.
- Robbins, C. S.; Bruun, B.; Zim, H. S. (1983) A guide to field identification: birds of North America. New York, NY: Golden Press.

2-76 Osprey

- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Spitzer, P. (1980) Dynamics of a discrete coastal breeding population of ospreys in the northeastern U.S. during a period of decline and recovery, 1969-1979 [Ph.D. dissertation]. Ithaca, NY: Cornell University.
- Spitzer, P. R.; Risebrough, R. W.; Walker, W. I.; et al. (1978) Productivity of ospreys in Connecticut Long Island increases as DDE residues decline. Science 202: 333-335.
- Stinson, C. H. (1977) Familial longevity in ospreys. Bird-Banding 48: 72-73.
- Stocek, R. F.; Pearce, P. A. (1983) Distribution and reproductive success of ospreys in New Brunswick, 1974-1980. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 215-221.
- Stotts, V. D.; Henny, C. J. (1975) The age at first flight for young American ospreys. Wilson Bull. 87: 277-278.
- Swenson, J. E. (1978) Prey and foraging behavior of ospreys on Yellowstone Lake, Wyoming. J. Wildl. Manage. 42: 87-90.
- Swenson, J. E. (1979) Factors affecting status and reproduction of ospreys in Yellowstone National Park. J. Wildl. Manage. 43: 595-601.
- Szaro, R. C. (1978) Reproductive success and foraging behavior of the osprey at Seahorse Key, Florida. Wilson Bull. 90: 112-118.
- Ueoka, M. L. (1974) Feeding behavior of ospreys at Humboldt Bay, California [master's thesis]. Arcata, CA: Humboldt State University.
- Van Daele, L. J.; Van Daele, H. A. (1982) Factors affecting the productivity of ospreys nesting in west-central Idaho. Condor 84: 292-299.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Whittemore, R. E. (1984) Historical overview of osprey at the Mattamuskeet National Wildlife Refuge: results from ten years of nest and productivity surveys. In: Westall, M. A., ed. Proceedings of the Southeastern U.S. and Caribbean Osprey Symposium; pp. 17-41.
- Wilcox (1944) (cited in Henny, 1988b) Univ. of State of N.Y. Bull. to the Schools 30:262-264.

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2.1.6. Red-Tailed Hawk (buteo hawks)

Order Falconiformes, Family Accipitridae. The family Accipitridae includes most birds of prey except falcons, owls, and American vultures. Buteo hawks are covered in this section.^b Buteo hawks are moderately large soaring hawks that inhabit open or semi-open areas. They are the most common daytime avian predators on ground-dwelling vertebrates, particularly rodents and other small mammals. They range in size from the broad winged hawk (41 cm bill tip to tail tip) to the ferruginous hawk (58 cm). Hawks egest pellets that contain undigestible parts of their prey, such as hair and feathers, that can be useful in identifying the types of prey eaten (bones usually are digested completely; Duke et al., 1987).

Selected species

The red-tailed hawk (*Buteo jamaicensis*) is the most common *Buteo* species in the United States (National Geographic Society, 1987). Breeding populations are distributed throughout most wooded and semiwooded regions of the United States and Canada south of the tundra (Adamcik et al., 1979), although some populations are found in deserts and prairie habitats. Six subspecies are recognized (Brown and Amadon, 1968). Nesting primarily in woodlands, red-tails feed in open country on a wide variety of small- to medium-sized prey.

Body size. Males of this medium-sized buteo (46 cm) weigh about 1 kg, and females are approximately 20 percent heavier than the males (see table). Otherwise, the sexes look alike (Brown and Amadon, 1968).

Habitat. Red-tails are found in habitats ranging from woodlands, wetlands, pastures, and prairies to deserts (Bohm 1978b; Gates, 1972; MacLaren et al., 1988; Mader, 1978). They appear to prefer a mixed landscape containing old fields, wetlands, and pastures for foraging interspersed with groves of woodlands and bluffs and streamside trees for perching and nesting (Brown and Amadon, 1968; Preston, 1990). Red-tails build their nests close to the tops of trees in low-density forests and often in trees that are on a slope (Bednarz and Dinsmore, 1982). In areas where trees are scarce, nests are built on other structures, occasionally in cactus (Mader, 1978), on rock pinnacles or ledges, or man-made structures (Brown and Amadon, 1968; MacLaren et al., 1988). In winter, night roosts usually are in thick conifers if available and in other types of trees otherwise (Brown and Amadon, 1968).

Food habits. Red-tails hunt primarily from an elevated perch, often near woodland edges (Bohm, 1978a; Janes, 1984; Preston, 1990). Small mammals, including mice, shrews, voles, rabbits, and squirrels, are important prey, particularly during winter. Red-tails also eat a wide variety of foods depending on availability, including birds, lizards, snakes, and large insects (Bent, 1937; Craighead and Craighead, 1956; Fitch et al., 1946). In general, red-tails are opportunistic and will feed on whatever species are most abundant

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^bOther members of the family Accipitridae, eagles and the osprey, are covered in Sections 2.1.7 and 2.1.5, respectively.

(Brown and Amadon, 1968). Winter food choices vary with snow cover; when small mammals such as voles become unavailable (under the snow), red-tails may concentrate on larger prey, such as pheasants (Gates, 1972).

Molt. Juveniles molt into adult plumage in a gradual process from the spring (age about 14 months) to summer or early fall (Bent, 1937).

Migration. The more northerly red-tailed hawk populations are migratory while the more southerly are year-round residents (Bent, 1937).

Breeding activities and social organization. Red-tails lay one clutch per year consisting of one to three eggs, although a replacement clutch is possible if the initial clutch is lost early in the breeding season (Bent, 1937). Their nests are large and built of twigs (Bohm, 1978b). Both sexes incubate, but the male provides food for the female during incubation and the entire family following hatching (Brown and Amadon, 1968). The parents continue to feed their young after fledging while they are learning to hunt (Brown and Amadon, 1968).

Home range and resources. Red-tailed hawks are territorial throughout the year, including winter (Brown and Amadon, 1968). Trees or other sites for nesting and perching are important requirements for breeding territories and can determine which habitats are used in a particular area (Preston, 1990; Rothfels and Lein, 1983). Home range size can vary from a few hundred hectares to over 1,500 hectares, depending on the habitat (Andersen and Rongstad, 1989; Petersen, 1979). In a 10-year study in Oregon, Janes (1984) found that the size of red-tail territories and the location of boundaries between territories varied little from year to year, even though individual birds or pairs died and were replaced.

Population density. Population densities generally do not exceed 0.03 pairs per hectare, and usually are lower than 0.005 pairs per hectare (see Appendix). Populations in southern areas such as Florida can increase substantially in the winter with the influx of migrants from the more northerly populations (Bohall and Collopy, 1984).

Population dynamics. Beginning at 2 years of age, most red-tailed hawks attempt to breed, although the proportion breeding can vary by population and environmental conditions (Henny and Wight, 1970, 1972). Average clutch size varies regionally, tending to increase from east to west and from south to north (Henny and Wight, 1970, 1972). In a 10-year study of red-tails in Alberta, Canada, Adamcik et al. (1979) found that the breeding population of adults remained stable despite strong cyclical fluctuations in the density of their main prey, the snowshoe hare, over the years. The mean clutch size for the red-tail population, however, appeared to vary with prey density, from 1.7 to 2.6 eggs/nest (Adamcik et al., 1979). Over the course of the study, about 50 percent of observed nestling losses occurred within 3 to 4 weeks after hatching due to starvation. Most of the variance in yearly mortality of nestlings could be attributed to the amount of food supplied and the frequency of rain. Large raptors such as horned owls also can be important sources of mortality for red-tail nestlings in some areas (Adamcik et al., 1979).

Similar species (from general references)

- The ferruginous hawk (*Buteo regalis*), one of the larger buteos (58 cm), inhabits the dry open country of the western United States.
- The red-shouldered hawk (*Buteo lineatus*) is slightly smaller (53 cm) and feeds on snakes, frogs, crayfish, mice, and some small birds. Its range is east of the Rocky Mountains and in California, with moist mixed woodlands preferred.
- Swainson's hawk (*Buteo swainsoni*) is restricted to the open plains of the western United States. Although it is as large (53 cm) as the red-tail, it preys mostly on insects.
- The broad-winged hawk (*Buteo platypterus*) is one of the smaller buteos (41 cm) and preys on mice, frogs, snakes, and insects. It prefers woodlands and is found almost exclusively east of the Mississippi River.
- Harris' hawk (*Parabuteo unicinctus*) is similar in size (53 cm) to the red-tailed hawk but is restricted to the semiarid wood and brushlands of the southwest. This bird nests in saguaro, mesquite, and yucca and preys on rodents, lizards, and small birds.
- The rough-legged hawk (*Buteo lagopus*) is one of the larger buteos (56 cm). It winters throughout most of the United States in open country but breeds only in the high arctic of North America.
- The zone-tailed hawk (Buteo albonotatus) is slightly smaller (51 cm) than most buteos and feeds on rodents, lizards, fish, frogs, and small birds. It can be found in mesa and mountain country within its limited range between the southwest United States and Mexico.
- The short-tailed hawk (*Buteo brachyurus*) is the smallest buteo (39 cm) and can only be found in the southern tip of Florida in mixed woodland and grassland habitats.

General references

Brown and Amadon (1968); Craighead and Craighead (1956); Fitch et al. (1946); National Geographic Society (1987).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A F A M	1,224 1,028		Michigan, Pennsylvania	Craighead & Craighead, 1956	
	A F A M	1,154 957		sw Idaho	Steenhof, 1983	
	A F A M hatchling F hatchling M juvenile F juvenile M	1,235 1,204 58 57 1,149 962		Ohio	Springer & Osborne, 1983	1
Metabolic Rate (IO₂/kg-day)	A B standard MR /spring	17.7 ± 5.9 SD		Michigan/metabolism chamber	Pakpahan et al., 1989	
Metabolic Rate (kcal/kg-day)	A F basal A M basal	73 77			estimated	2
	A M breeding A F breeding	109 102		California/mountains	Soltz, 1984	3
	A F free-living A M free-living	192 201	(91 - 408) (95 - 426)		estimated	4
Food Ingestion Rate (g/g-day)	A F winter A M winter A M summer	0.11 0.10 0.086		Michigan/captive outdoors	Craighead & Craighead, 1956	5
Water Ingestion Rate (g/g-day)	A F A M	0.055 0.059			estimated	6
Inhalation Rate (m³/day)	A F A M	0.48 0.42			estimated	7
Surface Area (cm²)	A F A M	1,147 1,021			estimated	8

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
summary of 10 years: snowshoe hare Richard's ground squirrel Franklin's ground squirrel voles & mice other mammals waterfowl ruffed grouse sharp-tailed grouse other grouse		mean ± SD 25.6 ± 19 30.4 ± 10 5.1 ± 2 4.8 ± 2 7.8 ± 6 16.2 ± 10 2.0 ± 2 1.2 ± 1 0.9 ± 1 6.3 ± 3			Alberta, Canada/ farm & woodlands (% wet weight of prey brought to chicks)	Adamcik et al., 1979	9
(mammals) Belding's ground squirrel mtn cottontail pocket gopher Townsend's ground squirrel (birds) Alectoris graeca western meadowlark (snakes) gopher snake	(78.5) 52.8 13.1 7.3 2.9 (8.5) 3.5 1.8 (13.1) 6.1				nc Oregon/ pasture and wheat fields (% wet weight of prey brought to nests; March to June)	Janes, 1984	9
ground squirrel rabbit pocket gopher other mammals gopher snake whiptail lizard birds		60.8 26.5 4.3 2.6 3.8 0.3 1.3			c California/foothills (% wet weight of prey brought to nests)	Fitch et al., 1946	9

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory	A B spring	60 - 160	Kange	c California/foothills	Fitch et al., 1946	NO.
Size (ha)	A B winter	697 ± 316 SD	381 - 989	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
	A B fall	1,770	957 - 2,465	Colorado/upland prairie, pinyon-juniper woodlands	Andersen & Rongstad, 1989	10
Population Density	summer: A B	pairs/ha: 0.0017 - 0.0050		Colorado/open aspen	McGovern & McNurney, 1986	
	A B area a A B area b	0.0004 0.0012	0.0002 - 0.0005 0.0010 - 0.0013	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
	АВ	0.0012	0.0010 - 0.0015	Alberta, Canada/farm, woodlands	Adamcik et al., 1979	
	winter: B B	N/ha: 0.014		Toronto, Canada/mixed old	Baker & Brooks, 1981	
	ВВ	0.0015 ± 0.0003 SD	0.0012 - 0.0018	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
Clutch Size		2.0 ± 0.77 SD 2.32 2.2 2.11 2.96	1 - 3 1.9 - 2.6 /10 yrs	c California/foothills Arizona/desert Alberta, Canada/farm, woodlands Florida/NS Oregon, Washington/NS	Fitch et al., 1946 Mader, 1978 Adamcik et al., 1979 Henny & Wight, 1972 Henny & Wight, 1970	
Clutches/Year		1			Bent, 1937	
Days Incubation		32		Alberta, Canada	Adamcik et al., 1979	

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Growth Rate	to 1 week 1 to 2 weeks 2 to 3 weeks 3 to 4 weeks 4 to 5 weeks	20 g/day 34 g/day 39 g/day 26 g/day 10 g/day		Ohio/free-living, habitat NS	Springer and Osborne, 1983	11
Age at Fledging		45 to 46 days		California/foothills	Fitch et al., 1946	
Number Fledge per Active Nest	high prey low prey	1.47 ± 0.25 SE 1.15 1.9 1.2	0.28 - 1.90/ 10 yrs	Oregon/pasture Alberta, Canada/farm, woodlands Idaho/canyon, shrub steppe	Janes, 1984 Adamcik et al., 1979 Steenhof & Kochert, 1985	
Number Fledge per Successful Nest		2.12 1.85		north of 42°N latitude/ North America south of 42°N latitude/ North America	Henny & Wight, 1970 Henny & Wight, 1970	12 12
Age at Sexual Maturity	В	2 years		throughout range	Henny & Wight, 1970	
Annual Mortality Rates (percent)	J B 1st year A B	62.4 20.6 ± 1.3 SE		north of 42°N latitude/ North America	Henny & Wight, 1970, 1972	13
	J B 1st year A B	66.0 23.9 ± 2.2 SE		south of 42°N latitude/ North America	Henny & Wight, 1970, 1972	13
Longevity			maximum 18 yrs	North America/NS	Henny & Wight, 1970, 1972	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	mid-February mid-April late March	early May	early April mid-May early April	Arizona Alberta Canada south Michigan	Mader, 1978 Luttich et al., 1971 Craighead & Craighead, 1956	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Hatching	late March mid-May late April	early June	early May mid-June early May	Arizona Alberta, Canada south Michigan	Mader, 1978 Luttich et al., 1971 Craighead & Craighead, 1956	
Fall Migration			mid-October	Montana, Alberta, Canada	Bent, 1937; Luttich et al., 1971	14
			late October late November	North Dakota Minnesota	Bent, 1937 Bent, 1937	
Spring Migration	late February mid-March early April	early March		south Michigan Maine, Montana Alberta, Canada	Craighead & Craighead, 1956 Bent, 1937 Luttich et al., 1971	15

- 1 Estimated from data provided by authors.
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Craighead and Craighead (1956).
- 3 Estimated from time and energy budgets for breeding season only.
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Craighead and Craighead (1956).
- Hawks maintained outdoors using falconer's techniques; fed lean raw beef supplemented with natural prey. Overall activity levels not described. Winter temperatures averaged 3 to 5°C and summer temperatures averaged 15°C during trials. Females weighed 1,218 g; males in winter weighed 1,147 g; males in summer weighed 855 g.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Craighead and Craighead (1956).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Craighead and Craighead (1956).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Craighead and Craighead (1956).
- 9 Percent biomass (wet weight) estimated from observations of prey brought to the nest (identified to species) and remains of prey found at the nests, using standard wet weights for each species of prey from other studies or measured in the lab.
- 10 Home range determined by 95 percent ellipse method; radio-tagged hawks, two of each sex.
- 11 Estimated from figure.
- 12 Summarizing data from several studies.
- 13 Summarizing banding recoveries prior to 1951.
- 14 Late departure dates.
- 15 Early arrival dates.

References (including Appendix)

- Adamcik, R. S.; Tood, A. W.; Keith, L. B. (1979) Demographic and dietary responses of red-tailed hawks during a snowshoe hare fluctuation. Can. Field-Nat. 93: 16-27.
- Andersen, D. E.; Rongstad, O. J. (1989) Home-range estimates of red-tailed hawks based on random and systematic relocations. J. Wildl. Manage. 53: 802-807.
- Baker, J. A.; Brooks, R. J. (1981) Distribution patterns of raptors in relation to density of meadow voles. Condor 83: 42-47.
- Bednarz, J. C.; Dinsmore, J. J. (1982) Nest-sites and habitat of red-shouldered and red-tailed hawks in Iowa. Wilson Bull. 94: 31-45.
- Bent, A. C. (1937) Life histories of North American birds of prey. Part 1: Order falconiformes. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 167.
- Bohall, P. G.; Collopy, M. W. (1984) Seasonal abundance, habitat use, and perch sites of four raptor species in north-central Florida. J. Field Ornithol. 55: 181-189.
- Bohm, R. T. (1978a) Observation of nest decoration and food habits of red-tailed hawks. Loon 50: 6-8.
- Bohm, R. T. (1978b) A study of nesting red-tailed hawks in central Minnesota. Loon 50: 129-137.
- Bosakowski, T.; Smith, D. G. (1992) Comparative diets of sympatric nesting raptors in the eastern deciduous forest biome. Can. J. Zool 70: 984-992.
- Brown, L.; Amadon, D. (1968) Eagles, hawks, and falcons of the world: v. 1. New York, NY: McGraw-Hill.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Craighead, J. J.; Craighead, F. C. (1956) Hawks, owls and wildlife. Harrisburg, PA: The Stackpole Co. and Washington, DC: Wildl. Manage. Inst.
- Duke, G. E.; Evanson, O. A.; Jegers, A. A. (1976) Meal to pellet intervals in 14 species of captive raptors. Comp. Biochem. Physiol. 53A: 1-6.
- Duke, G. E.; Mauro, L.; Bird, D. M. (1987) Physiology. In: Pendleton, B. A.; Millsap, B. A.; Cline, K. W.; et al., eds. Raptor management techniques manual. Washington, DC: Institute for Wildlife Research, National Wildlife Federation; Sci. Tech. Ser. No. 10; pp. 262-267.

- Fitch, H. S.; Swenson, F.; Tillotson, D. F. (1946) Behavior and food habits of the red-tailed hawk. Condor 48: 205-237.
- Gates, J. M. (1972) Red-tailed hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84: 421-433.
- Gatz, T. A.; Hegdal, P. L. (1987) Local winter movements of four raptor species in central Colorado. West. Birds 17: 107-114.
- Hagar, D. C., Jr. (1957) Nesting populations of red-tailed hawks and horned owls in central New York state. Wilson Bull. 69: 263-272.
- Hardy, R. (1939) Nesting habits of the western red-tailed hawk. Condor 41: 79-80.
- Henny, C. J.; Wight, H. M. (1970) Population ecology and environmental pollution: red-tailed and Cooper's hawks. Symposium: Population ecology of migratory birds; Patuxent Wildlife Research Center; pp. 229-249.
- Henny, C. J.; Wight, H. M. (1972) Population ecology and environmental pollution: red-tailed and Cooper's hawks. U.S. Bur. Sport Fish. Wildl., Wildl. Res. Rep. 2: 229-250.
- Janes, S. W. (1984) Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65: 862-870.
- Johnson, S. J. (1975) Productivity of the red-tailed hawk in southwestern Montana. Auk 92: 732-736.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Luttich, S. N.; Keith, L. B.; Stephenson, J. D. (1971) Population dynamics of the red-tailed hawk (*Buteo jamaicensis*) at Rochester, Alberta. Auk 88: 75-87.
- MacLaren, P. A.; Anderson, S. H.; Runde, D. E. (1988) Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Nat. 48: 548-553.
- Mader, W. J. (1978) A comparative nesting study of red-tailed hawks and Harris' hawks in southern Arizona. Auk 95: 327-337.
- McGovern, M.; McNurney, J. M. (1986) Densities of red-tailed hawk nests in aspen stands in the Piceance Basin, Colorado. Raptor Res. 20: 43-45.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.

- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Nice, M. M. (1954) Problems of incubation periods in North American birds. Condor 56: 173-197.
- Orians, G.; Kuhlman, J. (1956) The red-tailed hawk and great horned owl populations in Wisconsin. Condor 58: 371-385.
- Pakpahan, A. M.; Haufler, J. B.; Prince, H. H. (1989) Metabolic rates of red-tailed hawks and great horned owls. Condor 91: 1000-1002.
- Petersen, L. (1979) Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wisc. Dept. Nat. Resour. Tech. Bull. No. 111.
- Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.
- Preston, C. R. (1990) Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor 92: 107-112.
- Rothfels, M.; Lein, M. R. (1983) Territoriality in sympatric populations of red-tailed and Swainson's hawks. Can. J. Zool. 61: 60-64.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Smith, D. G.; Murphy, J. R. (1973) Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 18: 1-76.
- Soltz, R. L. (1984) Time and energy budgets of the red-tailed hawk (*Buteo jamaicensis*) in southern California. Southwest Nat. 29: 149-156.
- Springer, M. A.; Kirkley, J. S. (1978) Inter- and intraspecific interactions between red-tailed hawks and great horned owls in central Ohio. Ohio J. Sci. 78: 323-328.
- Springer, M. A.; Osborne, D. R. (1983) Analysis of growth of the red-tailed hawk (*Buteo jamaicensis*). Ohio J. Sci 83: 13-19.
- Steenhof, K. (1983) Prey weights for computing percent biomass in raptor diets. Raptor Res. 17: 15-27.
- Steenhof, K. (1987) Assessing raptor reproductive success and productivity. In: Giron Pendleton, B. A.; Millsap, B. A.; Cline, K. W., et al., eds. Raptor management techniques manual. Washington, DC: National Wildlife Federation; pp. 157-170.

- Steenhof, K.; Kochert, M. N. (1985) Dietary shifts of sympatric buteos during a prey decline. Oecologia 66: 6-16.
- U. S. Department of Interior. (1979) Snake River birds of prey special research report. Boise, ID: Bureau of Land Management.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

2.1.7. Bald Eagle (eagles)

Order Falconiformes, Family Accipitridae. Eagles have long rounded wings, large hooked bills, sharp talons, and are the largest birds of prey in the United States. They swoop down on their prey at high speeds, and their diet varies by species and considerably by habitat. In most species, the male is smaller than the female, but otherwise the sexes are similar in appearance. This family also includes kites and hawks.

Selected species

The bald eagle (*Haliaeetus leucocephalus*), our national symbol, is a federally designated endangered species. Relatively common in Alaska, populations in the lower 48 States have been seriously diminished, although they are recovering in some areas. Bald eagles are most commonly sighted in coastal areas or near rivers or lakes. Bald eagles are primarily carrion feeders.

Body size. Females are significantly larger than males, but otherwise the sexes look alike (Brown and Amadon, 1968). Body size increases with latitude and is the sole basis by which the northern and southern subspecies are divided (Snow, 1973). Length from bill tip to tail tip averages 81 cm in the more northerly populations.

Habitat. Bald eagles generally are restricted to coastal areas, lakes, and rivers (Brown and Amadon, 1968), although some may winter in areas not associated with water (Platt, 1976). Preferred breeding sites include proximity to large bodies of open water and large nest trees with sturdy branches (often conifers) and areas of old-growth timber with an open and discontinuous canopy (Andrew and Mosher, 1982; Anthony et al., 1982; Grubb, 1980; Peterson, 1986). In an analysis of more than 200 nests, Grubb (1980) found 55 percent within 46 m of a shoreline and 92 percent within 183 m of shore. During migration and in winter, conifers often are used for communal roosting both during the day and at night, perhaps to minimize heat loss (Anthony et al., 1982; Stalmaster, 1980). Mature trees with large open crowns and stout, horizontal perching limbs are preferred for roosting in general (Anthony et al., 1982; Chester et al., 1990). Bald eagles reach maximum densities in areas of minimal human activity and are almost never found in areas of heavy human use (Peterson, 1986).

Food habits. Primarily carrion feeders, bald eagles eat dead or dying fish when available but also will catch live fish swimming near the surface or fish in shallow waters (Brown and Amadon, 1968). In general, bald eagles can be described as opportunistic feeders, taking advantage of whatever food source is most plentiful and easy to scavenge or to capture, including birds and mammals (Brown and Amadon, 1968; Green, 1985; Watson et al., 1991). In many areas, especially in winter, waterfowl, killed or injured by hunters, and shore birds are an important food source (Todd et al., 1982). Eagles forage in upland areas in the winter when surface waters are frozen over, consuming carrion including rabbits, squirrels, and dead domestic livestock such as pigs and chickens (Brown and Amadon, 1968; Harper et al., 1988). Bald eagles also have been known to steal food from other members of their own species as well as from hawks, osprey, gulls, and mergansers (Grubb, 1971; Jorde and Lingle, 1988; Sobkowiak and Titman, 1989). This

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may occur when there is a shortage of a primary food source, such as fish, and an abundance of other prey such as waterfowl being used by other predatory birds (Jorde and Lingle, 1988). Some prey are important to a few populations; for example, in the Chesapeake Bay region, turtles are consumed during the breeding season (Clark, 1982), and at Amchitka Island in Alaska, sea otter pups are found regularly in bald eagle nests (Sherrod et al., 1975). In the Pacific Northwest during the breeding season, Watson et al. (1991) found that bald eagles hunted live prey 57 percent of the time, scavenged for 24 percent of their prey, and pirated 19 percent (mostly from gulls or other eagles). Because bald eagles scavenge dead or dying prey, they are particularly vulnerable to environmental contaminants and pesticides (e.g., from feeding on birds that died from pesticides, consuming lead shot from waterfowl killed or disabled by hunters) (Henny and Anthony, 1989; Harper et al., 1988; Lingle and Krapu, 1988). Bald eagles also are vulnerable to biomagnification of contaminants in food chains. For example, near Lake Superior (WI), herring gulls, which were consumed by over 20 percent of nesting bald eagle pairs, were found to be a significant source of DDE and PCB intake by the eagles (Kozie and Anderson, 1991). The gulls contained higher contaminant levels than the local fish because of their higher trophic level.

Molt. Adult eagles molt yearly. In northern populations, molting occurs from late spring to early fall; in southern populations, molting may be initiated earlier (McCollough, 1989). It is likely that the molt is not complete, and that some feathers are retained for 2 years. Young bald eagles generally molt into their adult plumage by their fifth year (McCollough, 1989).

Migration. Bald eagles migrate out of areas where lakes are completely frozen over in winter, but will remain as far north as the availability of open water and a reliable food supply allow (Brown and Amadon, 1968). Areas with ice-free waterways, such as the Columbia River estuary in Washington and Oregon, may support both resident and migratory populations in the winter (Watson et al., 1991). The far northern breeding populations migrate south for the winter and often congregate in areas with abundant food, particularly the Mississippi Valley and the northwestern States (Snow, 1973). Some populations of eagles that breed in southern latitudes (e.g., Arizona, Florida) show a reverse migration and migrate north in midsummer (following breeding), returning south in early autumn or winter (Brown and Amadon, 1968; Grubb et al., 1983).

Breeding activities and social organization. Bald eagles have been observed to nest successfully at 4 years of age, but most do not breed until at least their fifth year (Nye, 1983). Breeding pairs remain together as long as both are alive (Brown and Amadon, 1968). Large stick nests (approximately 1.5 m across and 0.6 m deep) are built near water and most often in a large tree, but sometimes on rocky outcrops or even on the ground on some islands (Brown and Amadon, 1968; Grubb, 1980). In the absence of disturbance, the same nest site may be used for many years (Nash et al., 1980). In Florida, eggs are laid in late autumn or winter, while over the rest of the eagle's range, mating and egg laying occur in spring (Brown and Amadon, 1968). Clutch sizes are larger in the north, and both sexes take responsibility for feeding the young (Brown and Amadon, 1968). Young fledge at about 10 to 12 weeks of age; after leaving the nest, they are still dependent on their parents for several weeks and often return to the nest for food (Sprunt et al., 1973). After nesting, large groups will often gather at sites with plentiful food

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resources, such as along rivers following a salmon spawn (Fitzner and Hanson, 1979; Keister et al., 1987; McClelland, 1973).

Home range and resources. During the breeding season, eagles require large areas in the vicinity of open water, with an adequate supply of nesting trees (Brown and Amadon, 1968). Distance from human disturbance is an important factor in nest site selection, and nests have been reported to fail as a result of disturbance (Andrew and Mosher, 1982). During incubation and brooding, eagles show territorial defense of an area around the nest site. Following fledging, there is little need for nest defense, and eagles are opportunistic in their search for abundant sources of prey (Mahaffy and Frenzel, 1987). During winter, eagles roost communally in large aggregations and share a foraging home range. For example, Opp (1980) described a population of 150 eagles that fed on meadow voles in a 250-ha flooded field for a 4-week period. This group also established a communal night roost in the vicinity.

Population density. Because population density depends strongly on the configuration of the surface water bodies used for foraging, few investigators have published explicit density estimates on an area basis; most report breeding densities along a shoreline on a linear basis. During the breeding season, 0.03 to 0.4 pairs have been recorded per km shore (see table). Eagles migrating south from their summer territories in Canada have aggregated in communal roosts of up to 400 eagles in a 40-ha area (Crenshaw and McClelland, 1989). In the winter, communal roost sites may also contain large numbers of eagles. Opp (1980) described a group of 150 eagles that roosted and foraged together in the Klamath Basin (OR/CA), and communal night roosts of up to 300 eagles in Oregon in late winter.

Population dynamics. Not all adults in an area are part of the breeding population. Some pairs may establish territories and not breed, while others may not even pair. The percentage of adults breeding and the breeding success of those that do vary with local food abundance, weather, and habitat conditions (Hansen, 1987; Hansen and Hodges, 1985; McAllister et al., 1986). In past years, bioaccumulation of organochlorine pollutants reduced the reproductive success of bald eagles. Now, in many areas, these raptors are reproducing at rates similar to those prior to the widespread use of these pesticides (Green, 1985). Eagles lay one clutch per year, although replacement clutches may be laid upon loss of the initial one (Sherrod et al., 1987). Very little is known about mortality rates of bald eagles; Grier (1980) concluded from population models that adult survival is more important than reproductive rate to the continued success of bald eagle populations. In captivity, bald eagles have lived for up to 50 years (Snow, 1973), and one wild eagle, banded and recaptured in Alaska, was estimated to be almost 22 years old (Cain, 1986). Upon loss of an initial clutch, bald eagles may lay replacement clutches if sufficient time remains (Sherrod et al., 1987).

Similar species (from general references)

• The golden eagle (Aquila chrysaetos) is similar in size (81 cm) to the bald eagle, and its range encompasses all but the southeastern United States. Small mammals, snakes, birds, and carrion are primary prey items, and golden eagles prefer mountainous or hilly terrain.

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General references

Brown and Amadon (1968); Green (1985); Peterson (1986); Stalmaster and Gessaman (1982, 1984).

Bald Eagle (Haliaeetus leucocephalus)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% Cl of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	J F summer J M summer	5,089 4,014	4,359 - 5,756 3,524 - 4,568	Alaska	Imler & Kalmbach, 1955	1
	A F A M	4,500 3,000		Florida	Wiemeyer, 1991 (pers. comm.) Krantz et al., 1970	
	egg egg	120.6 ± 8.2 SD 102.5 ± 17.9 SD	108 - 134 71 - 125	Wisconsin Florida	Krantz et al., 1970 Krantz et al., 1970	
	at hatching	91.5 ± 5.2 SD		Saskatchewan, Canada	Bortolotti, 1984b	
	nestlings: M 10 days M 30 days	500 (est.) 2,700 (est.)		Saskatchewan, Canada	Bortolotti, 1984a,b	2
	M 50 days M 60 days	3,600 (est.) 4,066 ± 35.1 SE	3,575 - 4,500		Bortolotti, 1984a,b	
	F 10 days F 30 days F 50 days	500 (est.) 3,000 (est.) 4,600 (est.)		Saskatchewan, Canada		2
Metabolic Rate (kcal/kg-day)	F 60 days free-living A winter	5,172 ± 46.5 SE	4,800 - 5,600	Connecticut	Craig et al., 1988	3
, ,	J winter A F free-living	111	(62 - 290)		estimated	4
	A M free-living	143	(66 - 307)		Communica	

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Factors	Age/ Cond	Sex/ d./Seas.	Mean		Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Food Ingestion Rate (g/g-day)	ВВ	er: salmon rabbit duck	0.092 ± 0.026 0.075 ± 0.013 0.065 ± 0.012	SD		Utah (captive)	Stalmaster & Gessaman, 1982	
	A B	adult B nile B	0.12 0.10 0.091			Washington (free-flying)	Stalmaster & Gessaman, 1984	5
	A B juve	nile B	0.12 0.14			Connecticut (free-flying)	Craig et al., 1988	6
Water Ingestion Rate (g/g-day)	A F A M		0.035 0.037				estimated	7
Inhalation Rate (m³/day)	A F A M		1.43 1.19				estimated	8
Surface Area (cm²)	A F A M		2,970 2,530				estimated	9
Dietary Composition		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Not No.
mallard American widge American coot other birds Chinook salmon sucker European carp other fish					32 9 9 3 21 4 1	Washington/river (% biomass; prey remains found below communal roost)	Fitzner & Hanson, 1979	

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Bald Eagle

other fish

other animals

24.0

24.0

Location/Habitat Dietary Note Composition Fall Winter No. Spring Summer (measure) Reference brown bullhead 24.8 Maine/inland river Todd et al., 1982 19.5 white sucker chain pickerel 20.1 (% occurrence in pellets) smallmouth bass 3.8 white perch 3.6 samples from all seasons other fish 4.9 except winter black duck 3.0 other birds 13.5 mammals 6.8 (57.6) central Arizona/desert Haywood & Ohmart, 1986 (fish) channel catfish 21.8 scrub, riparian Sonora sucker 8.6 carp 17.3 (% biomass; prey observed brought to nest or found at other fish 8.5 (birds) (14.1)nests) American coot 8.1 great blue heron 4.4 (mammals) (28.1)desert cottontail 8.1 14.9 jackrabbit rock squirrel 1.1 (reptiles) (0.2)15.5 pink salmon Alaska/coastal Ofelt, 1975 32.0 herring trout 4.5 (% frequency of occurrence;

prey observed brought to

the nest)

Bald Eagle (Haliaeetus leucocephalus)

Bald Eagle (Haliaeetus leucocephalus)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory Area (ha)	pair spring	3,494 ± 2,520 SD	1,821 - 6,392	Arizona/desert, riparian river	Haywood & Ohmhart, 1983	
Territory Length (km)	pair pair	3.5 15.8	1.4 - 7.2 11.1 - 26.6	Washington/SJ Islands; Grays Harbor	Grubb, 1980	
Territory Radius (km)	pair incubat. pair brooding	0.56 ± 0.18 SE 0.72 ± 0.21 SE		Minnesota/lake, woods	Mahaffy & Frenzel, 1987	
Winter Home Range (ha)	J B winter A B winter	1,830 ± 1,460 SD 1,880 ± 900 SD		Missouri/lake	Griffin & Baskett, 1985	
Foraging Distance (km)	B B winter	3 to 7		Connecticut/river	Craig et al., 1988	
Population Density	summer	0.38		se Alaska/riverine	Hansen, 1987	
(pair/km shore)	summer	0.035 0.026 0.045		WY, ID, MT/: Yellowstone Continental Snake	Swenson et al., 1986	
Clutch Size		2 2.3	1 - 3 1 - 4	NS/NS PA, DE, MD, NJ	Brown & Amadon, 1968 Schmid, 1966-67	
Clutches/Yea r		1		NS/NS	Sherrod et al., 1987	
Days Incubation		35	34 - 38	Maryland (captive)	Maestrelli & Wiemeyer, 1975	
Age at Fledging (days)	M F	79.9 ± 1.08 SE 83.0 ± 0.94 SE		Saskatchewan/lake	Bortolotti, 1989	
Number Fledge per Active Nest		1.01 1.28 0.90 1.14	0.58 - 1.22/10 yr 1.07 - 1.58/9 yr 0.76 - 1.14/7 yr	California/NS Montana/NS Washington/NS Florida/NS	Henny & Anthony, 1989 Henny & Anthony, 1989 Henny & Anthony, 1989 McEwan & Hirth, 1979	
		1.00 ± 0.06 SE	0 - 3	Alaska/NS	Sprunt et al., 1973	

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Number Fledge per Successful Nest		1.65 ± 0.26 SD 1.35 ± 0.11 SD 2.2 1.64	1.22 - 1.48/6 yr 1 - 3	Arizona/desert scrub, river Washington/San Juan Island PA, DE, MD, NJ/NS ID, MT, WY/river, lake	Grubb et al., 1983 Grubb et al., 1983 Schmid, 1966-67 Swenson et al., 1986	
Age at Sexual Maturity	В	4	3 - 5	United States/NS	Nye, 1983	
Annual Mortality (percent)	A B fledging to 1 yr	5.4 89.3		Alaska/Amchitka Island	Sherrod et al., 1977	
Longevity	AB		up to 50 yrs	captivity	Snow, 1973	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Layin g	late September December late October February early March late March	late December	November late January March late April early April	Florida, Texas Arizona se United States MD, VA, DE WY, MT, ID Vancouver BC	Mager, 1977 Grubb et al., 1983 USFWS, 1989 LeFranc & Cline, 1983 Swenson et al., 1986 Brown & Amadon, 1968	10
Fledging	April early July	late July late August	May mid-August	s Louisiana WY, MT, ID se Alaska	Harris et al., 1987 Swenson et al., 1986 Hansen, 1987	
Fall Migration	early October late October November	June November December/January December	mid-December January	Arizona Montana sc Oregon, n California se Alaska	Grubb et al., 1983 Crenshaw & McClelland, 1989 Keister et al., 1987 Hodges et al., 1987	
Spring Migration	late March	December April early April	,	Arizona sc Oregon, n California WY, MT, ID Illinois	Grubb et al., 1983 Keister et al., 1987 Swenson et al., 1986 Sabine, 1981	

- 1 Cited in Maestrelli and Wiemeyer (1975) and Bortolotti (1984a); juveniles up to 3 years of age. 2 Estimated from Figure 4.
- 3 Daily energy budget for free-living eagles based on time-activity budgets and metabolic models; assuming 4.5 kg eagle.
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Imler and Kalmbach (1955).
- 5 Estimated from observed captures of preweighed salmon provided at feeding stations. Eagle body weight assumed to be 4.5 kg. Some feeding may have occurred elsewhere.
- 6 Estimate of food consumed based on observed feeding behaviors and an eagle body weight of 4.5 kg.
- 7 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Imler and Kalmbach (1955).
- 8 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Imler and Kalmbach (1955).
- 9 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Imler and Kalmbach (1955).
- 10 Cited in Green, 1985.

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References (including Appendix)

- Andrew, J. M.; Mosher, J. A. (1982) Bald eagle nest site selection and nesting habitat in Maryland. J. Wildl. Manage. 46: 382-390.
- Anthony, R. G.; Knight, R. L.; Allen, G. T.; et al. (1982) Habitat use by nesting and roosting bald eagles in the Pacific Northwest. Trans. North Am. Wildl. Nat. Resour. Conf. 47: 332-342.
- Bortolotti, G. R. (1984a) Sexual size dimorphism and age-related size variation in bald eagles. J. Wildl. Manage. 48: 72-81.
- Bortolotti, G. R. (1984b) Physical development of nestling bald eagles with emphasis on the timing of growth events. Wilson Bull. 96: 524-542.
- Bortolotti, G. R. (1989) Factors influencing the growth of bald eagles in north central Saskatchewan. Can. J. Zool. 67: 606-611.
- Brown, L.; Amadon, D. (1968) Eagles, hawks, and falcons of the world: v. 1. New York, NY: McGraw-Hill.
- Cain, S. L. (1986) A new longevity record for the bald eagle. J. Field Ornithol. 57: 173.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Chester, D. N.; Stauffer, D. F.; Smith, T. J.; et al. (1990) Habitat use by nonbreeding bald eagles in North Carolina. J. Wildl. Manage. 54: 223-234.
- Chura, N. J.; Stewart, P. A. (1967) Care, food consumption, and behavior of bald eagles used in DDT tests. Wilson Bull. 79: 441-458.
- Clark, W. S. (1982) Turtles as a food source of nesting bald eagles in the Chesapeake Bay region. J. Field Ornithol. 53: 49-51.
- Craig, R. J.; Mitchell, E. S.; Mitchell, J. E. (1988) Time and energy budgets of bald eagles wintering along the Connecticut River. J. Field Ornithol. 59: 22-32.
- Crenshaw, J. G.; McClelland, B. R. (1989) Bald eagle use of a communal roost. Wilson Bull. 101: 626-633.
- Dugoni, J. A.; Zwank, P. J.; Furman, G. C. (1986) Food of nesting bald eagles in Louisiana. Raptor Res. 20: 124-127.
- Duke, G. E.; Evanson, O. A.; Jegers, A. A. (1976) Meal to pellet intervals in 14 species of captive raptors. Comp. Biochem. Physiol. 53A: 1-6.

- Duke, G. E.; Mauro, L.; Bird, D. M. (1987) Physiology. In: Pendleton, B. A.; Millsap, B. A.; Cline, K. W.; et al., eds. Raptor management techniques manual. Washington, DC: Institute for Wildlife Research, National Wildlife Federation; Sci. Tech. Ser. No. 10; pp. 262-267.
- Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.
- Dunstan, T. C.; Harper, J. F. (1975) Food habits of bald eagles in north-central Minnesota. J. Wildl. Manage. 39: 140-143.
- Dzus, E. H.; Gerrard, J. M. (1989) Interlake variations of bald eagle, *Haliaeetus leucocephalus*, populations in north-central Saskatchewan. Can. Field-Nat. 103: 29-33.
- Fielder, P. C. (1982) Food habits of bald eagles along the mid-Columbia River, Washington. Murrelet 63: 46-50.
- Fielder, P. C.; Starkey, R. G. (1980) Wintering bald eagle use along the upper Columbia River, Washington. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 177-193.
- Fitzner, R. E.; Hanson, W. C. (1979) A congregation of wintering bald eagles. Condor 81: 311-313.
- Fitzner, R. E.; Watson, D. G.; Rickard, W. (1980) Bald eagles of the Hanford National Environmental Research Park. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 207-218.
- Frenzel, R. W.; Anthony, R. G. (1989) Relationship of diets and environmental contaminants in wintering bald eagles. J. Wildl. Manage. 53: 792-802.
- Gessaman, J. A.; Fuller, M. R.; Pekins, P. J.; et al. (1991) Resting metabolic rate of golden eagles, bald eagles, and barred owls with a tracking transmitter or an equivalent load. Wilson Bull. 103: 261-265.
- Green, N. (1985) The bald eagle. Audubon Wildl. Rep. 508-531.
- Grier, J. W. (1977) Quadrant sampling of a nesting population of bald eagles. J. Wildl. Manage. 41: 438-443.
- Grier, J. W. (1980) Modeling approaches to bald eagle population dynamics. Wildl. Soc. Bull. 8: 316-322.
- Grier, J. W. (1982) Ban of DDT and subsequent recovery of reproduction in bald eagles. Science 218: 1232-1235.

2-102 Bald Eagle

- Griffin, C. R.; Baskett, T. S. (1985) Food availability and winter range sizes of immature and adult bald eagles. J. Wildl. Manage. 49: 592-594.
- Grubb, T. C. (1971) Bald eagles stealing fish from common mergansers. Auk 88: 928-292.
- Grubb, T. G. (1976) A survey and analysis of nesting bald eagles in western Washington [master's thesis]. Seattle, WA: University of Washington.
- Grubb, T. G. (1980) An evaluation of bald eagle nesting in western Washington. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 87-103.
- Grubb, T. G.; Hensel, R. J. (1978) Food habits of nesting bald eagles on Kodiak Island, Alaska. Murrelet 59: 70-72.
- Grubb, T. G.; Knight, R. L.; Rubink, D. M.; et al. (1983) A five year comparison of bald eagle productivity in Washington and Arizona. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 35-45.
- Hansen, A. J. (1987) Regulation of bald eagle reproductive rates in southeast Alaska. Ecology 68: 1387-1392.
- Hansen, A. J.; Hodges, J. I. (1985) High rates of non-breeding adult bald eagles in southeastern Alaska. J. Wildl. Manage. 49: 454-458.
- Harper; R. G.; Hopkins, D. S.; Dunstan, T. C. (1988) Nonfish prey of wintering bald eagles in Illinois. Wilson Bull. 100: 688-690.
- Harris, J. O.; Zwank, P. J.; Dugoni, J. A. (1987) Habitat selection and behavior of nesting bald eagles in Louisiana. J. Raptor Res. 21: 27-31.
- Haywood, D. D.; Ohmart, R. D. (1983) Preliminary report on habitat utilization by two pairs of breeding bald eagles in Arizona. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 87-94.
- Haywood, D. D.; Ohmart, R. D. (1986) Utilization of benthic-feeding fish by inland breeding bald eagles. Condor 88: 35-42.
- Henny, C. J.; Anthony, R. G. (1989) Bald eagle and osprey. Natl. Wildl. Fed. Sci. Tech. Ser. No. 12: 66-82.
- Hensel, R. J.; Troyer, W. A. (1964) Nesting studies of the bald eagle in Alaska. Condor 66: 282-286.
- Herrick, F. H. (1932) Daily life of the American eagle: early phase. Auk 49: 307-323.

- Hodges, J. I.; King, J. G. (1979) Resurvey of the bald eagle breeding population in southeast Alaska. J. Wildl. Manage. 43: 219-221.
- Hodges, J. I.; Boeker, E. L.; Hansen, A. J. (1987) Movements of radio-tagged bald eagles, Haliaeetus leucocephalus, in and from southeastern Alaska. Can. Field-Nat. 101: 136-140.
- Howard, R. P.; van Daele, L. J. (1980) An overview of the status of bald eagles in Idaho. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 23-34.
- Hulce, H. (1886) Eagles breeding in captivity. Forest and Stream 27: 327.
- Hulce, H. (1887) Eagles breeding in captivity. Forest and Stream 28: 392.
- Imler, R. H.; Kalmbach, E. R. (1955) The bald eagle and its economic status. U.S. Fish Wildl. Ser. Circ. 30.
- Jorde, D. G.; Lingle, G. R. (1988) Kleptoparasitism by bald eagles wintering in south-central Nebraska. J. Field Ornithol. 59: 183-188.
- Keister, G. P., Jr.; Anthony, R. G.; Holbo, H. R. (1985) A model of energy consumption in bald eagles: an evaluation of night communal roosting. Wilson Bull. 97: 148-160.
- Keister, G. P., Jr.; Anthony, R. G.; O'Neill, E. J. (1987) Use of communal roosts and foraging areas by bald eagles wintering in the Klamath Basin. J. Wildl. Manage. 51: 415-420.
- Kozie, K. D.; Anderson, R. K. (1991) Productivity, diet, and environmental contaminants in bald eagles nesting near the Wisconsin shoreline of Lake Superior. Arch. Environ. Contam. Toxicol. 20: 41-48.
- Krantz, W. C.; Mulhern, B. M.; Bagley, G. E.; et al. (1970) Organochlorine and heavy metal residues in bald eagle eggs. Pestic. Monit. J. 4: 136-40.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- LeFranc, M. N., Jr.; Cline, K. W. (1983) The occurrence of birds as prey at active bald eagle nests in the Chesapeake Bay region. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 79-86.
- Lingle, G. R.; Krapu, G. L. (1988) Ingestion of lead shot and aluminum bands by bald eagles during winter in Nebraska. Wilson Bull. 100: 326-327.
- Maestrelli, J. R.; Wiemeyer, S. N. (1975) Breeding bald eagles in captivity. Wilson Bull. 87: 45-53.

- Mager, D. (1977) The life and the future of the southern bald eagle. In: Proceedings of the bald eagle conference on eagle movements. Apple River, IL: Eagle Valley Environmentalists; pp. 115-117.
- Mahaffy, M. S.; Frenzel, L. D. (1987) Territorial responses of northern bald eagles near active nests. J. Wildl. Manage. 51: 551-554.
- McAllister, K. R.; Owens, T. E.; Leschner, L.; et al. (1986) Distribution and productivity of nesting bald eagles in Washington, 1981-1985. Murrelet 67: 45-50.
- McClelland, B. R. (1973) Autumn concentrations of bald eagles in Glacier National Park. Condor 75: 121-123.
- McCollough, M. A. (1989) Molting sequence and aging of bald eagles. Wilson Bull. 101: 1-10.
- McEwan, L. C.; Hirth, D. H. (1979) Southern bald eagle productivity and nest site selection. J. Wildl. Manage. 43: 585-594.
- McEwan, L. C.; Hirth, D. H. (1980) Food habits of the bald eagle in north-central Florida. Condor 82: 229-231.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Murphy, J. R. (1965) Nest site selection by the bald eagle in Yellowstone National Park. Proc. Utah Acad. Sci. Arts and Letters 12: 261-264.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- Nash, C.; Pruett-Jones, M.; Allen, T. G. (1980) The San Juan Islands bald eagle nesting survey. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 105-176.
- Nicholson, D. J. (1952) Little known facts about Florida bald eagles. Florida Nat. 25: 23-26.
- Nye, P. E. (1983) A biological and economic review of the hacking process for the restoration of bald eagles. In: Bird, D. M.; Seymour, N. R.; Gerrard, J. M., eds. Biology and management of bald eagles and ospreys. St. Anne de Bellvue, Quebec: Harpell Press; pp. 127-135.
- Ofelt, C. H. (1975) Food habits of nesting bald eagles in southeast Alaska. Condor 77: 337-338.
- Opp, R. R. (1980) Status of the bald eagle in Oregon 1980. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 35-48.

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- Peterson, A. (1986) Habitat suitability index models: bald eagle (breeding season). U.S. Fish Wildl. Serv. Biol. Rep. 82(10.126); 25 pp.
- Platt, J. B. (1976) Bald eagles wintering in Utah desert. American Birds 30: 783-788.
- Ricklefs, R. E. (1973) Fecundity, mortality and avian demography. In: Farner, D. S., ed. Breeding biology of birds. Washington, DC: National Academy of Sciences.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Sabine, N. (1981) Ecology of bald eagles wintering in southern Illinois [master's thesis] (abstract). Carbondale, IL: Southern Illinois University.
- Schmid, F. C. (1966-67) Numbers of eggs and young of bald eagles in four middle Atlantic states. Cassinia 50: 15-17.
- Sherrod, S. K.; Estes, J. A.; White, C. M. (1975) Depredation of sea otter pups by bald eagles at Amchitka Island, Alaska. J. Mammal. 56: 701-703.
- Sherrod, S. K.; White, C. M.; Williamson, F. S. (1977) Biology of the bald eagle on Amchitka Island, Alaska. Living Bird 15: 143-182.
- Sherrod, S. K.; Jenkins, M. A.; McKee, G.; et al. (1987) Using wild eggs for production of bald eagles for reintroduction into the southeastern United States. In: Odom, R. R.; Riddleberger, K. A.; Ozier, J. C., eds. Proceedings of the third southeastern nongame and endangered wildlife symposium; August; Athens, GA. Atlanta, GA: Georgia Dept. of Natural Resources; pp. 14-20.
- Snow, C. (1973) Habitat management series for endangered species report number 5: southern bald eagle *Haliaeetus leucocephalus leucocephalus* and northern bald eagle *Haliaeetus leucocephalus alascansus*. Denver, CO: Bureau of Land Management; BLM-YA-PT-81-019-6601.
- Snyder, N. F.; Wiley, J. W. (1976) Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20.
- Sobkowiak, S.; Titman, R. D. (1989) Bald eagles killing American coots and stealing coot carcasses from greater black-backed gulls. Wilson Bull. 101: 494-496.
- Sprunt, A., VI; Robertson, W. B., Jr.; Postupalsky, S.; et al. (1973) Comparative productivity of six bald eagle populations. Trans. North Am. Wildl. Nat. Resour. Conf. 38: 96-106.
- Stalmaster, M. V. (1980) Management strategies for wintering bald eagles in the Pacific Northwest. In: Knight, R. L.; Allen, G. T.; Stalmaster, M. V.; et al., eds. Proceedings of Washington bald eagle symposium, June; Seattle, WA. Seattle, WA: The Nature Conservancy; pp. 49-67.

- Stalmaster, M. V.; Gessaman, J. A. (1982) Food consumption and energy requirements of captive bald eagles. J. Wildl. Manage. 46: 646-654.
- Stalmaster, M. V.; Gessaman, J. A. (1984) Ecological energetics and foraging behavior of overwintering bald eagles. Ecol. Monogr. 54: 407-428.
- Stickel, L. F.; Chura, N. J.; Stewart, P. A.; et al. (1966) Bald eagle pesticide relations. Trans. North Am. Wildl. Natur. Resour. Conf. 21: 190-200.
- Swenson, J. E. (1975) Ecology of the bald eagle and osprey in Yellowstone National Park [master's thesis]. Bozeman, MT: Montana State University.
- Swenson, J. E.; Alt, K. L.; Eng, R. L. (1986) Ecology of bald eagles in the Greater Yellowstone ecosystem. Wildl. Monogr. 95: 1-46.
- Todd, C. S.; Young, L. S.; Owen, R. B., Jr.; et al. (1982) Food habits of bald eagles in Maine. J. Wildl. Manage. 46: 636-645.
- United States Fish and Wildlife Service (USFWS). (1989) Recovery plan: southeastern states bald eagle. Atlanta, GA: U.S. Fish and Wildlife Service, Southeast Region.
- Vermeer, K.; Morgan, K. H. (1989) Nesting population, nest sites, and prey remains of bald eagles in Barkley Sound, British Columbia. Northwest. Nat. 70: 21-26.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Watson, J. W.; Garrett, M. G.; Anthony, R. G. (1991) Foraging ecology of bald eagles in the Columbia River estuary. J. Wildl. Manage. 55: 492-499.
- Weaver, J. (1980) Habitat management program: threatened and endangered plants and animals. U.S. Forest Serv., Bridger-Teton Nat. Forest, Jackson Hole, WY; 111 pp.

2.1.8. American Kestrel (falcons)

Order Falconiformes, Family Falconidae. Falcons are the more streamlined of the raptor species, with long pointed wings bent back at the wrists and large tails that taper at the tips. They consume many kinds of animals including insects, reptiles, small mammals, and birds. Falcons are found in a variety of habitats, from cities to the most remote areas. Strong fliers that achieve high speeds, falcons range in size from the American kestrel (27 cm bill tip to tail tip) to the peregrine falcon (41 to 51 cm).

Selected species

The American kestrel (*Falco sparverius*), or sparrow hawk, is the most common falcon in open and semi-open areas throughout North America. There are three recognized subspecies: *F. s. paulus* (year-round resident from South Carolina to Florida and southern Alabama), *F. s. peninsularis* (year-round resident of southern Baja California), and *F. s. sparverius* (widespread and migratory) (Bohall-Wood and Collopy, 1986). Predators of the kestrel include large raptors such as great horned owls, golden eagles, and red-tailed hawks (Meyer and Balgooyen, 1987).

Body size. Weighing slightly over one tenth of a kilogram, the kestrel is the smallest falcon native to the United States (Brown and Amadon, 1968). As for most raptors, females are 10 to 20 percent larger than males (Bloom, 1973; Craighead and Craighead, 1956). Kestrel body weights vary seasonally, with maximum weight (and fat deposits) being achieved in winter and minimum weights in summer (Bloom, 1973; Gessaman and Haggas, 1987).

Habitat. Kestrels inhabit open deserts, semi-open areas, the edges of groves (Brown and Amadon, 1968), and even cities (National Geographic Society, 1987). In several areas, investigators have found that male kestrels tend to use woodland openings and edges, while females tend to utilize more open areas characterized by short or sparse ground vegetation, particularly during the winter (Koplin, 1973, cited in Mills, 1976; Meyer and Balgooyen, 1987; Mills, 1975, 1976; Smallwood, 1987). In other areas, however, investigators have found no such differentiation (Toland, 1987; Sferra, 1984). In Florida, kestrels appear to prefer sandhill communities (particularly pine/oak woodlands); these areas provide high-quality foraging habitat and the majority of available nest sites (Bohall-Wood and Collopy, 1986). Kestrels are more likely to use habitats close to centers of human activities than are most other raptors (Fischer et al., 1984).

Food habits. Kestrels prey on a variety of small animals including invertebrates such as worms, spiders, scorpions, beetles, other large insects, amphibians and reptiles such as frogs, lizards, and snakes, and a wide variety of small- to medium-sized birds and mammals (Brown and Amadon, 1968; Mueller, 1987). Large insects, such as grasshoppers, are the kestrels' primary summer prey, although in their absence kestrels will switch to small mammals (Collopy, 1973) and birds (Brown and Amadon, 1968). In winter, small mammals and birds comprise most of the diet (Collopy and Koplin, 1983; Koplin et al., 1980). Kestrels usually cache their vertebrate prey, often in clumps of grass or in tree limbs and holes, to be retrieved later (Collopy, 1977; Mueller, 1987; Rudolph, 1982; Toland,

1984). Invertebrate prey usually are eaten immediately (Rudolph, 1982). In Florida, where small mammals are scarce and reptiles are abundant, lizards are an important component of the diet (Bohall-Wood and Collopy, 1987). Kestrels forage by three different techniques: using open perches from which to spot and attack ground prey, hovering in the air to spot ground prey, and catching insects on the wing (Rudolph, 1982, 1983).

Molt. Females begin their molt during incubation and complete it by the end of the breeding season. Males, who are responsible for capturing most of the prey for the family, do not begin their molt until near the end of the breeding season (Smallwood, 1988).

Migration. The American kestrel is a year-round resident over most of the United States, but is migratory over the northern-most portions of its range (National Geographic Society, 1987). Because of their late molt, males migrate and arrive at the wintering grounds later than females or immatures (Smallwood, 1988).

Breeding activities and social organization. Adult kestrels are solitary, except during the breeding season, and maintain territories even in winter (Brown and Amadon, 1968). Kestrels typically build their nests in tree cavities, but have used holes in telephone poles, buildings, or stream banks when tree cavities are not available (Brown and Amadon, 1968). Both parents participate in incubation, but the female performs most of the incubation, while the male provides her with food (Brown and Amadon, 1968). Following hatching, the male brings the majority of the prey to the nestlings (Brown and Amadon, 1968). After fledging, young kestrels remain dependent on their parents for food for at least 2 to 4 additional weeks (Lett and Bird, 1987). Fledglings often perch and socialize with their siblings prior to dispersal (Lett and Bird, 1987). In Florida, resident kestrels (paulus subspecies) maintain year-round pair bonds and joint territories. The resident pairs have a competitive advantage over winter migrants (sparverius subspecies) in their territories (Bohall-Wood and Collopy, 1986).

Home range and resources. Although some investigators have not noted territorial defense (e.g., Craighead and Craighead, 1956), Mills (1975) demonstrated that kestrels defend territories by introducing captured birds into other birds' territories. Winter foraging territories range from a few hectares in productive areas (e.g., in California) (Meyer and Balgooyen, 1987) to hundreds of hectares in less productive areas (e.g., Illinois, Michigan) (Craighead and Craighead, 1956; Mills, 1975). Summer breeding territories probably follow the same pattern (Craighead and Craighead, 1956).

Population density. Although much smaller than red-tailed hawks and bald eagles, reported kestrel breeding population densities can be similarly low (e.g., 0.0003 to 0.004 nests per hectare; see table).

Population dynamics. Kestrels are sexually mature in the first breeding season after their birth (Carpenter et al., 1987). Scarcity of suitable nesting cavities probably limits the size of kestrel populations in parts of the United States (Cade, 1982). Three to four young may fledge per nest per year, but mortality of juveniles in the first year is high (60 to 90 percent) (Craighead and Craighead, 1956; Henny, 1972). Adult mortality can be low (e.g., 12 percent per year) (Craighead and Craighead, 1956).

Similar species (from general references)

- The peregrine falcon (*Falco peregrinus*), a rare resident of woods, mountains, and coasts, preys almost exclusively on birds. Though uncommon, they can be found wintering in most states, but rarely breeding. These large falcons (38 cm) have been reintroduced in some areas in the United States and have nested in urban environments.
- The merlin (Falco columbarius), larger (30 cm) than the kestrel, can be found
 in a variety of habitats but nests in open woods or wooded prairies.
 Wintering along coasts and near cities of the Great Plains, it primarily eats
 birds.
- The prairie falcon (Falco mexicanus) also is larger (39 to 50 cm) than the
 kestrel and inhabits dry, open country and prairies. A year-round resident of
 the western United States, prairie falcons prey chiefly on birds and small
 mammals.

General references

Cade (1982); Craighead and Craighead (1956); National Geographic Society (1987); Brown and Amadon (1968).

American Kestrel (Falco sparverius)

	Age/Sex/		Range or			Note
Factors	Cond./Seas.	Mean	(95% CI of mean)	Location	Reference	No.
Body Weight (g)	F fall F winter	115 ± 8.6 SD 132 ± 13 SD		California, Imperial Valley	Bloom, 1973	
	M fall M winter	103 ± 6.7 SD 114 ± 7.8 SD		California, Imperial Valley	Bloom, 1973	
	F laying/inc. F fall F winter	124 127 138		Utah	Gessaman & Haggas, 1987	
	M incubate M fall M winter	108 111 119		Utah	Gessaman & Haggas, 1987	
Metabolic Rate (kcal/kg-day)	F laying/inc. F fall F winter	414.4 ± 9.84 SE 368.7 ± 17.0 SE 327.2 ± 5.72 SE		Utah (free-living)	Gessaman & Haggas, 1987	1
	M incubate M fall M winter	337.6 ± 16.8 SE 364.9 ± 26.9 SE 386.4 ± 9.41 SE		Utah (free-living)	Gessaman & Haggas, 1987	1
	A F basal A M basal	134 140			estimated	2
	A M basal A F free-living A M free-living	333 345	(157 - 706) (162 - 733)		estimated	3
Food Ingestion Rate (g/g-day)	A B winter (vert. prey) (invert. prey)	0.29 (0.18) (0.11)		nw California (free-living)	Koplin et al., 1980	4
	A M summer	0.31		Ohio (seminatural enclosure)	Barrett & Mackey, 1975	
Water Ingestion Rate (g/g-day)	A F A M	0.11 0.12			estimated	5

American Kestrel

Factors Inhalation Rate (m³/day) Surface Area (cm²)	Age/S Cond. A F A M	ex/ /Seas.	Mean 0.089 0.079 267 242	Mean (0.089 0.079		or I of mean)	Location	Reference estimated estimated	Note No. 6
Dietary Composition		Spring	Summer	Fall	Winter	Location/Habitat (measure)		Reference	Note No.
invertebrates mammals birds reptiles other					32.6 31.7 30.3 1.9 3.5	California/open areas, woods (% wet weight of prey observed captured)		Meyer & Balgooyen, 1987	
vertebrates (primarily lizard invertebrates	vertebrates 49 (primarily lizards)					Florida/dry pine-oak woodlands (sandhill) (% wet weight of prey observed captured)		Bohall-Wood & Collopy, 1987	
frogs (Rana auro	other invertebrates frogs (<i>Rana aurora</i>) other herpetofauna <i>Microtus californicus Sorex vagrans</i>				10.8 14.2 8.0 12.2 30.2 9.4 11.5		hayfields, pasture ight of prey captured)	Collopy & Koplin, 1983	

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory Size (ha)	A F winter A M winter	31.6 ± 10.7 SD 13.1 ± 2.0 SD	18.7 - 42.0 9.7 - 14.8	California/open areas, woods	Meyer & Balgooyen, 1987	
	A B winter	154	< 452	Illinois/agricultural area	Mills, 1975	
	A B summer	202 ± 131 SD	41 - 500	Wyoming/grasslands, forests	Craighead & Craighead,	
	A B summer	131 ± 100 SD	21 - 215	Michigan/woodlots, fields	Craighead & Craighead, 1956	
Population Density	pairs summer pairs	0.0026 nests/ha 0.0004 nests/ha	0.0023 - 0.0031 0.0003 - 0.0006	Missouri/urban Missouri/rural	Toland & Elder, 1987 Toland & Elder, 1987	
	summer	0.0035 pairs/ha		Wyoming/grasslands, forest	Craighead & Craighead, 1956	
	pairs summer B B fall A B winter A B spring	birds/ha: 0.0007 ± 0.00004 SD 0.0005 ± 0.0001 SD 0.0010 ± 0.0002 SD	0.0005 - 0.0012 0.0005 - 0.0006 0.0008 - 0.0011	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
Clutch Size		4.3		California/juniper, sagebrush	Bloom & Hawks, 1983	
		4 to 5	3 - 7	NS/NS	Brown & Amadon, 1968	
Clutches/Year		1		Quebec, Canada/captive	Carpenter et al., 1987	
Days Incubation		33.7 ± 0.33 SE	33 - 35	Maryland/captive	Porter & Wiemeyer, 1972 Brown & Amadon, 1968	
		29 to 30		NS/NS		
Age at Fledging		27.4 days	26 - 30 days	Maryland/captive	Porter & Wiemeyer, 1972	

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Number Fledge per Active Nest		3.1 3.8		California/juniper, sagebrush Wyoming/grasslands, forest	Bloom & Hawks, 1983 Craighead & Craighead,	
Number Fledge per Successful Nest		3.7		California/juniper, sagebrush	1956 Bloom & Hawks, 1983	
Age at Sexual Maturity	В	1 yr		Quebec, Canada/captive	Carpenter et al., 1987	
Annual Mortality (percent)	A B J B	12 88		s Michigan, Wyoming/ open areas, woods	Craighead & Craighead, 1956	
	A B J B	46.0 ± 4.6 SE 60.7		North America/NS	Henny, 1972	
Longevity			up to 9 yrs	Quebec, Canada/captive	Carpenter et al., 1987	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/ Laying	early May mid-April early April	late May	late June early June mid-May	California central US northern Utah	Bloom & Hawks, 1983 Brown & Amadon, 1968 Gessaman & Haggas, 1987	
Hatching	early June early May	late June	early June late July mid-June	California northern Utah central Missouri	Brown & Amadon, 1968 Bloom & Hawks, 1983 Gessamen & Haggas, 1987 Toland & Elder, 1987	
Molt	mid-May		mid-September	northern Utah	Gessaman & Haggas, 1987	

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American Kestrel

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Migration fall spring	early September early March mid-April		early November	northern Utah south Michigan Wyoming	Gessaman & Haggas, 1987 Craighead & Craighead, 1956 Craighead & Craighead, 1956	

- 1 Investigators estimated values from time-activity budget studies of kestrels in the field and rates of energy expenditure during different activities measured in the laboratory.
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from winter measurements by Gessaman and Haggas (1987).
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from winter measurements by Gessaman and Haggas (1987).
- 4 Authors observed prey captured daily, and estimated total wet-weight prey intake using measured or reported weights for identifiable prey and estimated weights for unidentifiable invertebrate prey (also, assumed kestrel weighed 119 g). Also, see Chapters 3 and 4 for methods by estimating food ingestion rates.
- 5 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from winter measurements by Gessaman and Haggas (1987).
- 6 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from winter measurements by Gessaman and Haggas (1987).
- Festimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from winter measurements by Gessaman and Haggas (1987).

References (including Appendix)

- Barrett, G. W.; Mackey, C. V. (1975) Prey selection and caloric ingestion rate of captive American kestrels. Wilson Bull. 87: 514-519.
- Bird, D. M.; Clark, R. G. (1983) Growth of body components in parent- and hand-reared captive kestrels. Raptor Res. 17: 77-84.
- Bloom, P. H. (1973) Seasonal variation in body weight of sparrow hawks in California. Western Bird Bander 48: 17-19.
- Bloom, P. H.; Hawks, S. J. (1983) Nest box use and reproductive biology of the American kestrel in Lassen County, California. Raptor Res. 17: 9-14.
- Bohall-Wood, P.; Collopy, M. W. (1986) Abundance and habitat selection of two American kestrel subspecies in north-central Florida. Auk 103: 557-563.
- Bohall-Wood, P. G.; Collopy, M. W. (1987) Foraging behavior of southeastern American kestrels in relation to habitat use. Raptor Res. 6: 58-65.
- Brown, L.; Amadon, D. (1968) Eagles, hawks, and falcons of the world. New York, NY: McGraw Hill Book Co.
- Cade, T. J. (1982) The falcons of the world. Ithaca, NY: Cornell University Press.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Carpenter, J. W.; Gabel, R. R.; Wiemeyer, S. N.; et al. (1987) Captive breeding. In:
 Pendleton, B. A.; Millsap, B. A.; Cline, K. W.; et al., eds. Raptor management
 techniques manual. Washington, DC: National Wildlife Federation; pp. 350-355.
- Collopy, M. W. (1973) Predatory efficiency of American kestrels wintering in northwestern Califonia. Raptor Res. 7: 25-31.
- Collopy, M. W. (1977) Food caching by female American kestrels in winter. Condor 79: 63-68.
- Collopy, M. W.; Koplin, J. R. (1983) Diet, capture success, and mode of hunting by female American kestrels in winter. Condor 85: 369-371.
- Craighead, J. J.; Craighead, F. C. (1956) Hawks, owls and wildlife. Harrisburg, PA: The Stackpole Co. and Washington, DC: Wildlife Management Institute.
- Duke, G. E.; Evanson, O. A.; Jegers, A. A. (1976) Meal to pellet intervals in 14 species of captive raptors. Comp. Biochem. Physiol. 53A: 1-6.

- Duke, G. E.; Mauro, L.; Bird, D. M. (1987) Physiology. In: Pendleton, B. A.; Millsap, B. A.; Cline, K. W.; et al., eds. Raptor management techniques manual. Washington, DC: Institute for Wildlife Research, National Wildlife Federation; Sci. Tech. Ser. No. 10; pp. 262-267.
- Enderson, J. H. (1960) A population study of the sparrow hawk in east-central Illinois. Wilson Bull. 72: 222-231.
- Fischer, D. L.; Ellis, K. L.; Meese, R. J. (1984) Winter habitat selection of diurnal raptors in central Utah. Raptor Res. 18: 98-102.
- Gessaman, J. A. (1979) Premigratory fat in the American kestrel. Wilson Bull. 91: 625-262.
- Gessaman, J. A.; Haggas, L. (1987) Energetics of the American kestrel in northern Utah. Raptor Res. 6: 137-144.
- Henny, C. J. (1972) An analysis of the population dynamics of selected avian species with special reference to changes during the modern pesticide era. Washington, DC: Bur. Sport. Fish. Wildl.; Wildl. Res. Rep. 1.
- King, J. R. (1974) Seasonal allocation of time and energy resources in birds. In: Paynter, R. A., Jr., ed. Avian energetics. Cambridge, MA: Nuttall Ornithol. Club; pp. 4-70.
- Koplin, J. R. (1973) Differential habitat use by sexes of American kestrels wintering in northern California. Raptor Res. 7: 39-42.
- Koplin, J. R.; Collopy, M. W.; Bammann, A. R.; et al. (1980) Energetics of two wintering raptors. Auk 97: 795-806.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Lett, D. W.; Bird, D. M. (1987) Postfledging behavior of American kestrels in southwestern Quebec. Wilson Bull. 99: 77-82.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Meyer, R. L.; Balgooyen, T. G. (1987) A study and implications of habitat separation by sex of wintering American kestrels (*Falco sparverius* L.). Raptor Res. 6: 107-123.
- Mills, G. S. (1975) A winter population study of the American kestrel in central Ohio. Wilson Bull. 87: 241-247.
- Mills, G. S. (1976) American kestrel sex ratios and habitat separation. Auk 93: 740-748.

- Mueller, H. C. (1987) Prey selection by kestrels: a review. Raptor Res. 6: 83-106.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Porter, R. D.; Wiemeyer, S. N. (1972) Reproductive patterns in captive American kestrels (sparrow hawks). Condor 74: 46-53.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Rudolph, S. G. (1982) Foraging strategies of American kestrels during breeding. Ecology 63: 1268-1276.
- Rudolph, S. G. (1983) Aerial insect-catching by American kestrels. Condor 85: 368-369.
- Sferra, N. J. (1984) Habitat selection by the American kestrel (*Falco sparverius*) and red-tailed hawk (*Buteo jamaicensis*) wintering in Madison County, Kentucky. Raptor Res. 18: 148-150.
- Smallwood, J. A. (1987) Sexual segregation by habitat in American kestrels wintering in southcentral Florida: vegetative structure and responses to differential prey availability. Condor 89: 842-849.
- Smallwood, J. A. (1988) A mechanism of sexual segregation by habitat by American kestrels (*Falco sparverius*) wintering in south-central Florida. Auk 105: 36-46.
- Sparrowe, R. D. (1972) Prey-catching behavior in the sparrow hawk. J. Wildl. Manage. 36: 279-308.
- Toland, B. R. (1984) Unusual predatory and caching behavior of American kestrels in central Missouri. Raptor Res. 18: 107-110.
- Toland, B. R. (1987) The effect of vegetative cover on foraging strategies, hunting success and nesting distribution of American kestrels in central Missouri. Raptor Res. 21: 14-20.
- Toland, B. R.; Elder, W. H. (1987) Influence of nest-box placement and density on abundance and productivity of American kestrels in central Missouri. Wilson Bull. 99: 712-717.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Wing, L.; Wing, A. H. (1939) Food consumption of a sparrow hawk. Condor 41: 168-170.

- Zar, J. H. (1968) Standard metabolism comparisons between orders of birds. Condor 70: 278.
- Zar, J. H. (1969) The use of the allometric model for avian standard metabolism body weight relationships. Comp. Biochem. Physiol. 29: 227-234.

2.1.9. Northern Bobwhite (quail)

Order Galliformes, Family Phasiadinae. Quail are ground-dwelling birds with short, heavy bills adapted for foraging on the ground for seeds and insects. Most species inhabit brush, abandoned fields, and open woodlands; some inhabit parklands. Quail and most other gallinaceous birds are poor flyers that seldom leave the ground and do not migrate. All species of this family gather in coveys (i.e., flocks of varying size) during some part of the year. Quail range in size from Montezuma's quail (22 cm bill tip to tail tip) to the mountain and Gambel's quail (28 cm); sexes are similar in size but differ in appearance.

Selected species

The northern bobwhite (*Colinus virginianus*) feeds mainly on seeds by gleaning on the ground and low vegetation. It ranges from southeastern Wyoming, east to southern Minnesota and across to southern Maine, south through the central and eastern United States to eastern New Mexico in the west and to Florida in the east (American Ornithologists' Union, 1983). It is the most widespread of the North American quail and used to be very common, particularly east of the Rocky Mountains. Over the past three decades, however, populations have been declining throughout its range (Brennan, 1991).

Body size. Northern bobwhite are average-sized quail (25 cm). Wild bobwhites typically weigh between 150 and 200 g depending on location and season (see table), while commercially bred stock usually exceed 200 g and may reach 300 g or more (Brenner and Reeder, 1985; Koerth and Guthery, 1991). Males and females are similar in size, and weights tend to increase with latitude and toward the west coast of the United States (Hamilton, 1957; Rosene, 1969; Roseberry and Klimstra, 1971). Females are heaviest in the spring and summer when they are laying eggs; males are lightest at this time of year (Hamilton, 1957; Roseberry and Klimstra, 1971). Juveniles tend to weigh slightly less than adults through winter (Hamilton, 1957; Roseberry and Klimstra, 1971). Koerth and Guthery (1987) found both males and females to maintain between 9 and 11 percent body fat (as a percentage of dry body weight) throughout the year in southern Texas; more northern populations may maintain higher body fat ratios, particularly just prior to breeding (McRae and Dimmick, 1982).

Habitat. During the breeding season, grasslands, idle fields, and pastures are the preferred nesting habitat, and bobwhite often nest in large clumps of grasses (Roseberry and Klimstra, 1984). Shade, open herbaceous cover, and green and growing vegetation are required for suitable nest sites (Lehmann, 1984). Bobwhites forage in areas with open vegetation, some bare ground, and light litter (Stoddard, 1931). Nearby dry powdery soils are important for dust bathing (Johnsgard, 1988). Shrubby thickets up to 2 m high are used for cover during midday (Schroeder, 1985). Although their range is extensive, northern bobwhite reproduce poorly in the arid western portions of their range and during droughts elsewhere (Schroeder, 1985). During the winter, they require wooded cover with understory for daytime cover, preferably adjacent to open fields for foraging (Yoho and Dimmick, 1972). They tend to roost at night in more open habitats with short and sparse vegetation (Schroeder, 1985). In the more northern latitudes, cover and food can be limited during the winter (Rosene, 1969). Changes in land use, primarily

the distribution of farms and farming methods, have eliminated large areas of bobwhite habitat in the last three decades (Brennan, 1991).

Food habits. Bobwhites forage during the day, primarily on the ground or in a light litter layer less than 5 cm deep (Rosene, 1969). Seeds from weeds, woody plants, and grasses comprise the majority of the adult bobwhite's diet throughout the year (Handley, 1931; Bent, 1932; Lehmann, 1984), although in winter in the south, green vegetation has been found to dominate the plant materials in their diet (Campbell-Kissock et al., 1985). Insects and other invertebrates can comprise up to 10 to 25 percent of the adults' diet during the spring and summer in more northerly areas and year-round in the south (Campbell-Kissock et al., 1985; Handley, 1931; Lehmann, 1984). Insects comprise the bulk of the chicks' diet: up to 2 or 3 weeks of age chicks may consume almost 85 percent insects, the remainder of the diet consisting of berries and seeds (Handley, 1931). Most insects consumed by bobwhite chicks are very small, less than 8 mm in length and 0.005 g (Hurst, 1972). Juvenile bobwhite, on the other hand, may consume only 25 percent insects, the remainder of their diet being fruit and seeds (Handley, 1931). Quail consume little grit. Korschgen (1948) found grit in only 3.4 percent of over 5,000 crops examined, and agreed with Nestler (1946) that hard seeds can replace grit as the grinding agent for northern bobwhite.

In some areas, bobwhites apparently can acquire their daily water needs from dew, succulent plants, and insects (Stoddard, 1931); in more arid areas or in times of drought, however, northern bobwhite need surface water for drinking (Johnsgard, 1988; Lehmann, 1984; Prasad and Guthery, 1986). Females need more water than males during the breeding season, and both sexes may require more water in the winter than in the summer when their diet is more restricted to seeds with low water content (Koerth and Guthery, 1990). Measurements on captive quail have indicated a daily water requirement of up to 13 percent of their body mass (see table); however, water intake requirements for free-ranging birds may be higher, perhaps 14 to 21 percent of body mass per day (Koerth and Guthery, 1990). In the absence of adequate water, females may fail to reproduce (Koerth and Guthery, 1991).

Dustbathing. Quail frequently dustbathe, although the reason for the behavior is debated.^c They scratch in dry dirt or dust, toss the dust up into their feathers, rub their head and sides in the dust, and then shake the dust from their plumage (Borchelt and Duncan, 1974). Experiments by Driver et al. (1991) indicate that ingestion of materials preened from feathers and direct dermal uptake can be significant exposure pathways for quail exposed to aerial application of pesticides. Dust bathing might, therefore, provide a significant exposure route for bobwhites using contaminated soils.

Molt. Juveniles attain adult plumage during their first fall molt at about 3 to 5 months of age (Hamilton, 1957; Stoddard, 1931). Adults undergo a complete prebasic

^cStoddard (1931) and others have suggested that dust bathing helps to control ectoparasites; Borchelt and Duncan (1974) suggest that dust bathing helps control the amount of oil on the quails' feathers.

molt in the late summer and fall into winter plumage; in spring, a limited renewal of feathers around the head and throat provides the breeding plumage (Bent, 1932).

Migration. The northern bobwhite is a year-round resident over its entire range but may disperse locally to a different cover type or altitude with the changing season (Lehmann, 1984). Most winter in wooded or brushy areas, returning to more open habitats in spring for the breeding season (Lehmann, 1984; Rosene, 1969). Populations nesting at higher elevations tend to move to lower ground where the winters are less severe (Stoddard, 1931). The more southerly populations may be more sedentary; in a study in Florida, northern bobwhite were found no further than 1 km from where they were banded, and 86 percent were found within 400 m from their banding site over a 1- to 5-year period (Smith et al., 1982).

Breeding activities and social organization. Northern bobwhite build nests on the ground in open woodlands or in or around fields used for foraging. Most nests are constructed in grassy growth near open ground, often in areas with scattered shrubs and herbaceous growth (Klimstra and Roseberry, 1975; Stoddard, 1931). Both the male and female scrape out a saucer-shaped depression in the ground 2 to 6 cm deep and 10 to 12 cm across, lining it with dead grasses from the previous year's growth (Bent, 1932; Rosene, 1969). They lay large clutches, 12 to 30 eggs, which one or both parents incubate for approximately 23 days (Lehmann, 1984; Simpson, 1976). As a general rule, clutch size and nest success both decrease as the season progresses (Roseberry and Klimstra, 1984). Family units, consisting of both the male and female as well as the offspring, sometimes remain intact through the summer, but more often, one or both parents are lost to predation (some females leave their brood to the male and begin another), and other pairs or individual adults may adopt chicks from other broods (Lehmann, 1984). By fall, northern bobwhites of all ages gather in larger coveys for the fall and winter. The quail remain in coveys until the next spring, when they disperse as mating season begins (Lehmann, 1984; Roseberry and Klimstra, 1984). Coveys of northern bobwhite tend to average 10 to 12 or 15 birds (up to 30) (Johnsgard, 1988; Lehmann, 1984; Rosene, 1969). When roosting in winter, the birds in a covey form a small circle on the ground under a tree or in thick brush, with heads facing outward and their bodies closely packed to conserve heat.

Home range and resources. In the breeding season, the bobwhite's home range includes foraging areas, cover, and the nest site and may encompass several hectares. Mated males and incubating females have the smallest spring and summer home ranges; bachelor males and post-nesting males and females have much larger foraging ranges (see table). Bobwhite tend to use a portion of their home range more intensively than the remainder of the range (Urban, 1972). In the fall and winter, the range of each bobwhite covey must include adequate open foraging areas and cover, typically shrubby or woody thickets (Rosene, 1969). Each covey may utilize an area of several hectares, although as in summer, there tend to be activity centers where the quail spend most of their time (Yoho and Dimmick, 1972).

Population density. Bobwhite density depends on food and cover availability and varies from year to year as well as from one location to another (Roseberry and Klimstra, 1984). Densities are highest at the end of the breeding season in the fall. In the

southeast, densities may reach values as high as 7.5 birds (adults and juveniles) per hectare, although average values of 2 to 3 may be more common in these areas (Guthery, 1988; Lehmann, 1984; Smith et al., 1982). Winter and spring densities between 0.1 and 0.8 birds per hectare have been recorded in the spring further north (Roseberry et al., 1979).

Population dynamics. Bobwhites attempt to rear one or two broods per year (up to three in the south) (Bent, 1932; CKWRI, 1991; Stanford, 1972b). Bobwhite clutch sizes are generally smaller in more southerly populations (Roseberry and Klimstra, 1984) and smaller as the breeding season progresses in any given locale (Lehmann, 1984; Simpson, 1976). Predation is a major cause of nest loss; once hatched, chicks leave the nest immediately to follow both or one parent (Lehmann, 1984; Roseberry and Klimstra, 1984). Juveniles can survive without parental care after about 6 weeks of age (Lehmann, 1984). They reach maturity by 16 weeks of age in the laboratory although they continue to gain weight through about 20 weeks (Moore and Cain, 1975), and they may require 8 to 9 months to mature in the wild (Johnsgard, 1988; Jones and Hughes, 1978). Adult mortality as well as juvenile mortality is high, with 70 to 85 percent of birds surviving less than 1 year (Brownie et al., 1985; Lehmann, 1984); thus, the bulk of the population turns over each year.

Similar species (from general references)

- California quail (Callipepla californica), also known as valley quail, are similar in size (25 cm) to the bobwhite and also gather in coveys during autumn and winter. They are common in open woodlands, brushy foothills, stream valleys, and suburbs, usually near permanent surface waters; however, their range is restricted largely to the western coastal States and Baja California.
- Gambel's quail (*Callipepla gambelii*) is larger (28 cm) than the bobwhite, and is a resident of the southwestern desert scrublands, usually near permanent surface waters. It also gathers in coveys in winter.
- The scaled quail (*Callipepla squamata*), similar in size (25 cm) to the bobwhite, is restricted to the mesas, plateaus, semidesert scrublands, and grasslands mixed with scrub, primarily of western Texas, New Mexico, and Mexico.
- Mountain quail (*Oreortyx pictus*) are found in the chapparal, brushy ravines, and mountain slopes of the west up to 3,000 m. These also are large quail (28 cm). During the fall, they gather in coveys and descend to lower altitudes for the winter.
- The Montezuma quail (*Cyrtonyx montezumae*), formerly known as the harlequin quail, is a small (22 cm), secretive resident of the southwest. This species is usually found in grassy undergrowth of juniper or oak-pine woodlands.

General references

Johnsgard (1988); Lehmann (1984); National Geographic Society (1987); Rosene (1969); Roseberry and Klimstra (1984); Stoddard (1931).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	A B fall A B winter A B spring	189.9 ± 3.28 SE 193.9 ± 4.56 SE 190.0 ± 4.98 SE		Kansas	Robel, 1969	
	A M winter A M summer A F winter A F summer	181 163 183 180		Illinois	Roseberry & Klimstra, 1971	
	A M winter A M summer A F winter A F summer	161 154 157 157		west Rio Grande, Texas	Guthery et al., 1988	
	at hatching day 6 day 10 day 19 day 32 day 43 day 55 day 71 day 88 day 106	6.3 9 - 10 10 - 13 20 - 25 35 - 45 55 - 65 75 - 85 110 - 120 125 - 150 140 - 160	(weight gain:) (0.5 - 0.75 g/day) (1.5 g/day) (1.75 g/day) (1.75 - 2.0 g/day)	southwest Georgia/both captive and wild birds living in farms, woods, and thickets	Stoddard, 1931	
Body Fat (% dry weight)	J B fall A M winter A M spring A F winter	174.0 ± 3.49 SE 15.5 ± 2.8 SD 8.8 ± 3.2 SD 13.8 ± 2.7 SD		Kansas Tennessee	Robel, 1969 McRae & Dimmick, 1982	
Body Fat (% dry weight) (continued)	A F spring A M winter A M spring A F winter A F spring	12.7 ± 2.4 SD 10.2 ± 0.6 SE 7.9 ± 0.2 SE 10.6 ± 0.8 SE 9.7 ± 0.3 SE	9.0 - 11.9 6.5 - 10.0 8.3 - 19.9 7.7 - 11.2	southern Texas/captive	Koerth & Guthery, 1987	

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% Cl of mean)	Location or subspecies	Reference	Note No.
Egg Weight (grams)		9.3 ± 0.3 SE 8.6	8.0 - 10.2	Texas southwest Georgia	Koerth & Guthery, 1991 Stoddard, 1931	
Metabolic Rate (kcal/kg-day)	A F nonbreed A F laying	183.3 243.9		Nebraska/captive	Case, 1982	1
	A M basal A F basal	129 125			estimated	2
	A M free-living A F free-living	320 311	(151 - 677) (147 - 659)		estimated	3
Food Ingestion Rate (g/g-day)	A B winter A B spring A B summer A B fall	0.093 ± 0.0032 SE 0.067 ± 0.0021 SE 0.079 ± 0.0061 SE 0.072 ± 0.0017 SE		southern Texas/captive	Koerth & Guthery, 1990	4
(kcal/kg-day)	A B winter A B fall A B spring	587 657 519		Kansas	Robel, 1969	5
Water Ingestion Rate	A M summer A F summer	0.10 ± 0.023 SD 0.13 ± 0.037 SD		southern Texas/captive	Koerth & Guthery, 1990	
(g/g-day)	A M summer A F summer	0.11 0.10			estimated	6
Inhalation Rate (m³/day)	A M summer A F summer	0.10 0.11			estimated	7
Surface Area (cm²)	A M summer A F summer	298 320			estimated	8

Dietary					Location/Habitat		Note
Composition	Spring	Summer	Fall	Winter	(measure)	Reference	No.
adults:							
(total plant foods)	(87.2)	(78.7)	(79.7)	(96.8)	southeastern United	Handley, 1931	
misc. seeds	21.1	6.0	11.1	2.6	States/NS		
other seeds:							
legumes	15.2	3.9	10.1	31.5	(% volume; crop and gizzard		
senna	7.2	0.4	0.2	12.8	contents)		
cultivated plants	2.1	2.1	5.3	2.6			
grasses	3.1	11.3	26.0	2.3			
sedges	1.1	1.2	2.4	1.1			
mast	14.1	0.2	0.5	28.0			
spurges	0.1	1.2	5.5	0.4			
fruits	11.1	45.8	11.3	9.5			
forage plants	12	0.3	0.3	5.2			
(total animal foods)	(12.8)	(19.6)	(20.3)	(3.2)			
grasshoppers	3.2	7.5	16.6	2.4			
bugs	2.8	4.4	0.6	0.1			
beetles	4.6	6.3	8.0	0.2			
adults:							
seeds of weeds	43.64	33.7	30.0	34.3	south Texas/semi-prairie,	Lehmann, 1984	
seeds of weeds	4.03	20.5	39.7	9.5	brushland	Leimain, 1304	
plants	13.2	24.8	0.7	7.2	brusilialiu		
seeds of grasses	3.7	1.9	8.3	15.4	(% dry volume; crop		
cultivated grains, etc.	27.4	4.9	3.4	10.3	contents)		
greens	8.03	14.2	17.9	23.3	Contents)		
insects	0.00	14.2	17.5	20.0			
adults:							
seeds of forbs		3.5	19.0	12.0	southwest	Campbell-Kissock et al., 1985	
seeds of grasses		51.7	42.9	4.9	Texas/grasslands	Campbell-Nissock et al., 1905	
seeds of grasses seeds/fruits of		31.7	42.3	4.3	drought conditions		
woody plants		9.7	_	1.4	arought conditions		
unidentified seeds		4.6	_	2.3	(% wet volume; crop		
green vegetation		4.8	1.8	72.4	contents)		
invertebrates		25.8	36.2	6.5	contents)		

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Home Range	summer:					
Size (ha/bird)	AB	3.6		Iowa/State game area	Crim & Seitz, 1972	
	A M mated	7.6 ± 5.0 SD		south Illinois/idle farms	Urban, 1972	
	A M unmated	16.7 ± 9.5 SD		woods, brush, cornfields	·	
	A F nesting	6.4 ± 4.0 SD				
	A F post-nest	15.6 ± 9.1 SD				
(ha/covey)	winter:					
(ВВ	6.8 ± 2.9 SD	4.0 - 11.7	Tennessee/woods, old fields	Yoho & Dimmick, 1972	
	ВВ	15.4	12.1 - 18.6	cultivated fields south Illinois/NS	Bartholomew, 1967	
Damedation			1211 1010			
Population Density	B B fall	0.21 ± 0.0031 SE		south Texas/upland rangeland	Guthery, 1988	
(N/ha)	B B spring	0.10 ± 0.0003 SE				
	B B fall	0.63 ± 0.24 SD	0.28 - 0.92	south Illinois/agricultural	Roseberry et al., 1979	
	B B spring	0.24 ± 0.05 SD	0.18 - 0.33			
	B B fall	5.0 ± 0.30 SE		south Texas/mixed brush	Guthery, 1988	
	B B spring	2.2 ± 0.21 SE		rangeland		
	B B winter	0.63 ± 0.18 SD	0.37 - 0.88	South Carolina/farms,	Rosene, 1969	
				woods		
	B B winter	2.25 ± 1.16 SD	0.6 - 3.9		Smith et al., 1982	
	B B winter	3.65 ± 2.22 SD	1.7 - 7.6	Florida/pine woods		
Clutch Size		12.9	4 - 33	south Texas/prairie, brush	Lehmann, 1984	
0.01011 0.120		13.7 ± 3.28 SD	6 - 28	Illinois/agricultural	Roseberry & Klimstra, 1984	
	March	25.0		southwest Georgia/pine	Simpson, 1976	
	August	9.4		woods, farms		
Clutches/Year		1	0 - 3	NS/NS	CKWRI, 1991	
Days Incubation		23	21 - 25	south Texas/prairie, brush	Lehmann, 1984	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Percent Nests Successful		17.5	15.4 - 19.0	southwest Georgia/pine woods, farms	Simpson, 1976	
		32.6 ± 8.1 SD	21.0 - 52.8	south Illinois/agricultural	Roseberry & Klimstra, 1984	
Number Hatch per	1, 3			south Texas/semiprairie,	Lehmann, 1984	
Successful Nest	March August	20.0 8.4		southwest Georgia/pine woods, farms	Simpson, 1976	
Age at Sexual Maturity	B B	8 - 9 months 16 weeks		NS/NS (wild) South Carolina/lab	Johnsgard, 1988 Jones & Hughes, 1978	
Annual Mortality Rates (percent)	AM AF JM JF	78.8 ± 2.47 SE 85.3 ± 2.72 SE 81.8 ± 2.46 SE 87.2 ± 1.68 SE	64.7 - 94.8 68.4 - 98.6 73.0 - 93.7 67.9 - 95.8	Florida/open woods	Brownie et al., 1985	
	ВВ	81		Illinois/agricultural	Roseberry & Klimstra, 1984	
	no hunting B M B F	52 56		Florida/pine woods	Pollock et al., 1989	
Longevity (months)	starting: B November B October	10.6 8.5		Texas/semiprairie, brush central Missouri/NS	Lehmann, 1984 Marsden & Baskett, 1958	9
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/ Laying	March mid-April April	May - June mid-May - July	August mid-August September	Florida south Texas south Illinois	Bent, 1932 Lehmann, 1984 Roseberry & Klimstra, 1984	
Hatching	mid-March late April early May mid-May	May - June May - August mid-June June - August	mid-September October October early October	south Texas sw Georgia, northern Florida Missouri south Illinois	Lehmann, 1984 Stoddard, 1931 Stanford, 1972a Roseberry & Klimstra, 1984	

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Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Molt fall	August	September	October	NS	Bent, 1932	
spring	early February	March - April	early June	sw Georgia, northern Florida	Stoddard, 1931	

- 1 Metabolized energy requirements of farm-raised birds in captivity: (1) 7 weeks prior to laying (mean weight of hens = 194 g) and (2) during laying (mean weight of hens = 215 g).
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and summer body weights from Roseberry and Klimstra (1971).
- 3 Estimated using equation 3-37 (Nagy, 1987) and summer body weights from Roseberry and Klimstra (1971).
- 4 Diet of commercial game food with only 5 to 10 percent water content; maintained at temperature, humidity, and light cycle typical for Texas.
- 5 Gross energy intake calculated from the average volume of crop contents in shot birds, assuming a 1.5-hour retention period, 2.30 kcal/cm³ for the contents, and constant foraging throughout the daylight hours, which is likely to overestimate food intake.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Roseberry and Klimstra (1971).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Roseberry and Klimstra (1971).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Roseberry and Klimstra (1971).
- 9 Expected remaining longevity for those juvenile quail that survived to the month indicated.

References (including Appendix)

- American Ornithologists' Union. (1983) Check-list of North American birds. Lawrence, KS: Allen Press, Inc.
- Andrews, T. L.; Harms, R. H.; Wilson, H. R. (1973) Protein requirement of the bobwhite chick. Poult. Sci. 52: 2199-2201.
- Baldwin, W. P., Jr.; Handley, C. O. (1946) Winter food of the bobwhite quail in Virginia. J. Wildl. Manage. 10: 142-149.
- Bartholomew, R. M. (1967) A study of the winter activity of the bobwhite through the use of radiotelemetry. Kalamazoo, MI: Occas. Pap. Adams Ecol. Center, Western Mich. Univ.; 25 pp.
- Bent, A. C. (1932) Life histories of North American gallinaceous birds. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 162.
- Blem, C. R.; Zara, J. (1980) The energetics of young bobwhite (*Colinus virginianus*). Comp. Biochem. Physiol. A: Comp. Physiol. 67: 611-615.
- Borchelt, P. L.; Duncan, L. (1974) Dustbathing and feather lipid in bobwhite (*Colinus virginianus*). Condor 76: 471-472.
- Brennan, L. A. (1991) How can we reverse the northern bobwhite decline? Wildl. Soc. Bull. 19: 544-555.
- Brenner, F. J.; Reeder, M. (1985) Effect of temperature on energy intake in three strains of bobwhite quail (*Colinus virginianus*). Proc. Penn. Acad. Sci. 59: 119-120.
- Brownie, C.; Anderson, D. R.; Burnham, K. P.; et al. (1985) Statistical inference from band recovery data a handbook. Washington, DC: U.S. Fish Wildl. Serv., Resour. Publ. 156.
- Buss, I. O.; Mattison, H.; Kozlik, F. M. (1947) The bobwhite quail in Dunn County, Wisconsin. Wisc. Cons. Bull. 12: 6-13.
- Caesar Kleberg Wildlife Research Institute (CKWRI). (1991) Double broods revisited. In:
 Quail news from CKWRI No. 14, March 1991. Kingsville, TX: Texas A&I University; p.
 6.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Campbell-Kissock, L.; Blankenship, L. H.; Stewart, J. W. (1985) Plant and animal foods of bobwhite and scaled quail in southwest Texas. Southwest. Nat. 30: 543-553.

- Case, R. M. (1973) Bioenergetics of a covey of bobwhites. Wilson Bull. 85: 52-59.
- Case, R. M. (1982) Adaptations of female bobwhites to energy demands of the reproductive cycle. Proc. Natl. Bobwhite Quail Symp. 2: 74-78.
- Case, R. M.; Robel, R. J. (1974) Bioenergetics of the bobwhite. J. Wildl. Manage. 38: 638-652.
- Craighead, J. J.; Craighead, F. C. (1956) Hawks, owls and wildlife. Harrisburg, PA: The Stackpole Co. and Washington, DC: Wildlife Management Institute.
- Crim, L. A.; Seitz, W. K. (1972) Summer range and habitat preferences of bobwhite quail on a southern Iowa State Game Area. Proc. Iowa Acad. Sci. 79: 85-89.
- Driver, C. J.; Ligotke, M. W.; Van Voris, P.; et al. (1991) Routes of uptake and their relative contribution to the toxicologic response of northern bobwhite (*Colinus virginianus*) to an organophosphate pesticide. Environ. Toxicol. Chem. 10: 21-33.
- Guthery, F. S. (1988) Line transect sampling of bobwhite density on rangeland: evaluation and recommendations. Wildl. Soc. Bull. 16: 193-203.
- Guthery, F. S.; Koerth, N. E.; Smith, D. S. (1988) Reproduction of northern bobwhites in semiarid environments. J. Wildl. Manage. 52: 144-149.
- Hamilton, M. (1957) Weights of wild bobwhites in central Missouri. Bird Banding 28: 222-228.
- Handley, C. O. (1931) The food and feeding habits of bobwhites. In: Stoddard, H. L., ed. The bobwhite quail: its habits, preservation and increase. New York, NY: Charles Scribner's Sons.
- Heitmeyer, M. E. (1980) Foods of bobwhites in northeastern Missouri related to land use. Trans. Missouri Acad. Sci. 14: 51-60.
- Hurst, G. A. (1972) Insects and bobwhite quail brood habitat management. Proc. Natl. Bobwhite Quail Symp. 1: 65-82.
- Johnsgard, P. A. (1988) The quails, partridges, and francolins of the world. Oxford, England: Oxford University Press; pp. 60-68.
- Jones, J. E.; Hughes, B. L. (1978) Comparison of growth rate, body weight, and feed conversion between *Cortunix* D₁ quail and bobwhite quail. Poult. Sci. 57: 1471-1472.
- Judd, S. (1905) The bob-white and other quails of the United States and their economic relations. U.S. Biol. Survey Bull. 21: 1-66.
- Kellogg, F. E.; Doster, G. L.; Williamson, L. L. (1970) A bobwhite density greater than one bird per acre. J. Wildl. Manage. 34: 464-466.

- Klimstra, W. D.; Roseberry, J. L. (1975) Nesting ecology of the bobwhite in southern Illinois. Wildl. Monogr. 41; 37 pp.
- Koerth, N. E.; Guthery, F. S. (1987) Body fat levels of northern bobwhites in south Texas. J. Wildl. Manage. 51: 194-197.
- Koerth, N. E.; Guthery, F. S. (1990) Water requirements of captive northern bobwhites under subtropical seasons. J. Wildl. Manage. 54: 667-672.
- Koerth, N. E.; Guthery, F. S. (1991) Water restriction effects on northern bobwhite reproduction. J. Wildl. Manage. 55: 132-137.
- Korschgen, L. J. (1948) Late-fall and early-winter food habits of bobwhite quail in Missouri. J. Wildl. Manage. 12: 46-57.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967) A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.
- Lay, D. W. (1954) Quail management for east Texas. Texas Parks Wildl. Dept. Bull. No. 34.
- Lehmann, V. W. (1984) Bobwhites in the Rio Grande plain of Texas. College Station, TX: Texas A&M University Press.
- Marsden, H. M., Baskett, T. S. (1958) Annual mortality in a banded bobwhite population. J. Wildl. Manage. 22: 414-419.
- Martin, A. C.; Zim, H. S.; Nelson, A. L. (1951) American wildlife and plants. New York, NY: McGraw-Hill Book Company, Inc.
- McRae, W. A.; Dimmick, R. W. (1982) Body fat and blood-serum values of breeding wild bobwhites. J. Wildl. Manage. 46: 268-271.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Moore, P. E.; Cain, J. R. (1975) Characterization of bobwhite quail reared for hunting. Poult. Sci. 54: 1798.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Nelson, A. L.; Martin, A. C. (1953) Gamebird weights. J. Wildl. Manage. 17: 36-42.

- Nestler, R. B. (1946) Mechanical value of grit for bobwhite quail. J. Wildl. Manage. 10: 137-142.
- Nice, M. (1910) Food of the bobwhite. J. Economic Entomology 3: 6-10.
- Pollock, K. H.; Moore, C. T.; Davidson, W. R.; et al. (1989) Survival rates of bobwhite quail based on band recovery analyses. J. Wildl. Manage. 53: 1-6.
- Prasad, N. L.; Guthery, F. S. (1986) Drinking by northern bobwhites in Texas. Wilson Bull. 98: 485-486.
- Reid, V. H.; Goodrum, P. D. (1960) Bobwhite quail: a product of longleaf pine forests. Trans. North Am. Wildl. Conf. 25: 241-252.
- Robel, R. J. (1969) Food habits, weight dynamics and fat content of bobwhites in relation to food plantings in Kansas. J. Wildl. Manage. 38: 653-664.
- Robel, R. J.; Bisset, A. R.; Dayton, A. D.; et al. (1979a) Comparative energetics of bobwhites on six different foods. J. Wildl. Manage. 43: 987-992.
- Robel, R. J.; Bisset, A. R.; Clement, T. M., Jr.; et al. (1979b) Metabolizable energy of important foods of bobwhites in Kansas. J. Wild. Manage. 43: 982-987.
- Robel, R. J.; Case, R. M.; Bisset, A. R.; et al. (1974) Energetics of food plots in bobwhite management. J. Wildl. Manage. 38: 653-664.
- Roseberry, J. L.; Klimstra, W. D. (1971) Annual weight cycles in male and female bobwhite quail. Auk 88: 116-123.
- Roseberry, J. L.; Klimstra, W. D. (1984) Population ecology of the bobwhite. Carbondale and Edwardsville, IL: Southern Illinois University Press.
- Roseberry, J. L.; Peterjohn, B. G.; Klimstra, W. D. (1979) Dynamics of an unexploited bobwhite population in deteriorating habitat. J. Wildl. Manage. 43: 306-315.
- Rosene, W. (1969) The bobwhite quail, its life and management. New Brunswick, NJ: Rutgers Press.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Schroeder, R. L. (1985) Habitat suitability models index: northern bobwhite. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.104).
- Sermons, W. O.; Speake, D. W. (1987) Production of second broods by northern bobwhites. Wilson Bull. 99: 285-286.

- Simpson, R. C. (1976) Certain aspects of the bobwhite quails life history in southwest Georgia. Atlanta, GA: Georgia Dept. Nat. Resour.; Tech. Bull. WL1.
- Smith, G. F.; Kellogg, F. I.; Doster, G. L.; et al. (1982) A 10-year study of bobwhite quail movement patterns. Proc. Natl. Bobwhite Quail Symp. 2: 35-44.
- Stanford, J. A. (1972a) Bobwhite quail population dynamics: relationships of weather, nesting, production patterns, fall population characteristics, and harvest in Missouri quail. Proc. Natl. Bobwhite Quail Symp. 1: 115-139.
- Stanford, J. A. (1972b) Second broods in bobwhite quail. Proc. Natl. Bobwhite Quail Symp. 1: 21-27.
- Stempel, M. E. (1960) Quail hatching and primary feather moult in adults. Proc. lowa Acad. Sci. 67: 616-621.
- Stoddard, H. L. (1931) The bobwhite quail: its habits, preservation and increase. New York, NY: Charles Scribner's Sons.
- Tomlinson, R. E. (1975) Weights and wing lengths of wild Sonoran masked bobwhites during fall and winter. Wilson Bull. 87: 180-186.
- Urban, D. (1972) Aspects of bobwhite quail mobility during spring through fall months. Proc. Natl. Bobwhite Quail Symp. 1: 194-199.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Wiseman, D. S.; Lewis, J. C. (1981) Bobwhite use of habitat in tallgrass rangeland. Wildl. Soc. Bull. 9: 248-255.
- Wood, K. N.; Guthery, F. S.; Koerth, N. E. (1986) Spring-summer nutrition and condition of northern bobwhites in south Texas. J. Wildl. Manage. 50: 84-88.
- Yoho, N. S.; Dimmick, R. W. (1972) Habitat utilization by bobwhite quail during winter. Proc. Natl. Bobwhite Quail Symp. 1: 90-99.

2.1.10. American Woodcock (woodcock and snipe)

Order Charadriformes, Family Scolopacidae. These inland members of the sandpiper family have a stocky build, long bill, and short legs. However, their habitats and diet are distinct. Woodcock inhabit primarily woodlands and abandoned fields, whereas snipe are found in association with bogs and freshwater wetlands. Both species use their long bills to probe the substrate for invertebrates. The woodcock and snipe are similar in length, although the female woodcock weighs almost twice as much as the female snipe.

Selected species

The American woodcock (*Scolopax minor*) breeds from southern Canada to Louisiana throughout forested regions of the eastern half of North America. The highest breeding densities are found in the northern portion of this range, especially in the Great Lakes area of the United States, northern New England, and southern Canada (Gregg, 1984; Owen et al., 1977). Woodcock winter primarily in the southeastern United States and are year-round residents in some of these areas. Woodcock are important game animals over much of their range (Owen et al., 1977).

Body size. Woodcock are large for sandpipers (28 cm bill tip to tail tip), and females weigh more than males (Keppie and Redmond, 1988). Most young are full grown by 5 to 6 weeks after hatching (Gregg, 1984).

Habitat. Woodcock inhabit both woodlands and abandoned fields, particularly those with rich and moderately to poorly drained loamy soils, which tend to support abundant earthworm populations (Cade, 1985; Owen and Galbraith, 1989; Rabe et al., 1983a). In the spring, males use early successional open areas and woods openings, interspersed with low brush and grassy vegetation, for singing displays at dawn and dusk (Cade, 1985; Keppie and Redmond, 1985). Females nest in brushy areas of secondary growth woodlands near their feeding areas, often near the edge of the woodland or near a break in the forest canopy (Gregg, 1984). During the summer, both sexes use second growth hardwood or early successional mixed hardwood and conifer woodlands for diurnal cover (Cade, 1985). At night, they move into open pastures and early successional abandoned agricultural fields, including former male singing grounds, to roost (Cade, 1985; Dunford and Owen, 1973; Krohn, 1970). During the winter, woodcock use bottomland hardwood forests, hardwood thickets, and upland mixed hardwood and conifer forests during the day. At night, they use open areas to some degree, but also forested habitats (Cade, 1985). Diurnal habitat and nocturnal roosting fields need to be in close proximity to be useful for woodcock (Owen et al., 1977).

Food habits. Woodcocks feed primarily on invertebrates found in moist upland soils by probing the soil with their long prehensile-tipped bill (Owen et al., 1977; Sperry, 1940). Earthworms are the preferred diet, but when earthworms are not available, other soil invertebrates are consumed (Miller and Causey, 1985; Sperry, 1940; Stribling and Doerr, 1985). Some seeds and other plant matter may also be consumed (Sperry, 1940). Krohn (1970) found that during summer most feeding was done in wooded areas prior to entering fields at night, but other studies have indicated that a significant amount of food

is acquired during nocturnal activities (Britt, 1971, as cited in Dunford and Owen, 1973). Dyer and Hamilton (1974) found that during the winter in southern Louisiana, woodcock exhibited three feeding periods: early morning (0100 to 0500 hours) in the nocturnal habitat, midday (1000 to 1300 hours) in the diurnal habitat, and at dusk (1700 to 2100 hours) again in the nocturnal fields; earthworms and millipedes were consumed in both habitat types. Most of the woodcocks' metabolic water needs are met by their food (Mendall and Aldous, 1943, as cited in Cade, 1985), but captive birds have been observed to drink (Sheldon, 1967). The chicks leave the nest soon after hatching, but are dependent on the female for food for the first week after hatching (Gregg, 1984).

Molt. Woodcock molt twice annually. The prenuptial molt involves body plumage, some wing coverts, scapulars, and tertials and occurs in late winter or early spring; the complete postnuptial molt takes place in July or August (Bent, 1927).

Migration. Fall migration begins in late September and continues through December, often following the first heavy frost (Sheldon, 1967). The migration may take 4 to 6 weeks (Sheldon, 1967). Some woodcock winter in the south Atlantic region, while those that breed west of the Appalachian Mountains winter in Louisiana and other Gulf States (Martin et al., 1969, as cited in Owen et al., 1977). Woodcock are early spring migrants, leaving their wintering grounds in February and arriving on their northern breeding grounds in late March to early April (Gregg, 1984; Sheldon, 1967; Owen et al., 1977). Dates of woodcock arrival at their breeding grounds vary from year to year depending on the timing of snowmelt (Gregg, 1984). Sheldon (1967) summarizes spring and fall migration dates by States from numerous studies.

Breeding activities and social organization. From their arrival in the spring, male woodcock perform daily courtship flights at dawn and at dusk, defending a site on the singing grounds in order to attract females for mating (Owen et al., 1977; Gregg, 1984). Often several males display on a single singing ground, with each defending his own section of the area. Females construct their nests on the ground, usually at the base of a tree or shrub located in a brushy area adjacent to an opening or male singing ground (Gregg and Hale, 1977; McAuley et al., 1990; Owen et al., 1977). Females are responsible for all of the incubation and care of their brood (Trippensee, 1948). The young leave the nest soon after hatching and can sustain flight by approximately 18 days of age (Gregg, 1984).

Home range and resources. The home range of woodcocks encompasses both diurnal cover areas and nocturnal roosting areas and varies in size depending on season and the distribution of feeding sites and suitable cover. During the day, movements are usually limited until dusk, when woodcock fly to nocturnal roost sites. Hudgins et al. (1985) and Gregg (1984) found spring and summer diurnal ranges to be only 1 to 10 percent of the total home range. Movement on the nocturnal roost sites also is limited; however, during winter, woodcock are more likely to feed and move around at night (Bortner, pers. comm.). Singing males generally restrict their movements more than non-singing males, juveniles, and females (Owen et al., 1977).

Population density. The annual singing-ground survey conducted by the United States and Canada provides information on the population trends of woodcock in the

northern states and Canada during the breeding season (note from B. Bortner, U.S. Fish and Wildlife Service, Office of Migrating Bird Management, to Susan Norton, January 9, 1992). Gregg (1984) summarized results of several published singing-ground surveys and found estimates to vary from 1.7 male singing grounds per 100 ha in Minnesota (Godfrey, 1974, cited in Gregg, 1984) to 10.4 male singing grounds per 100 ha in Maine (Mendall and Aldous, 1943, cited in Gregg, 1984). Although this method is appropriate for assessing population trends, flushing surveys, telemetry, and mark-recapture are better methods for estimating woodcock densities because there are variable numbers of females and nonsinging males associated with active singing grounds (Dilworth, Krohn, Riffenberger, and Whitcomb pers. comm., cited by Owen et al., 1977). For example, Dwyer et al. (1988) found 2.2 singing males per 100 ha in a wildlife refuge in Maine, but with mark-recapture techniques, they found yearly summer densities of 19 to 25 birds per 100 ha in the same area.

Population dynamics. Woodcocks attempt to raise only a single brood in a given year but may renest if the initial clutch is destroyed (McAuley et al., 1990; Sheldon, 1967). In 12 years of study in Wisconsin, Gregg (1984) found 42 percent of all nests to be lost to predators and another 11 percent lost to other causes. Survival of juveniles in their first year ranges from 20 to 40 percent, and survival of adults ranges from 35 to 40 percent for males to approximately 40 to 50 percent for females (Dwyer and Nichols, 1982; Krohn et al., 1974). Derleth and Sepik (1990) found high adult survival rates (0.88 to 0.90 for both sexes) between June and October in Maine, indicating that adult mortality may occur primarily in the winter and early spring. They found lower summer survival rates for young woodcock between fledging and migration than for adults during the same months, with most losses of young attributed to predation.

Similar species (from general references)

• The common snipe (Gallinago gallinago) is similar in length (27 cm) to the woodcock, although lighter in weight. Snipe are primarily found in association with bogs and freshwater wetlands and feed on the various invertebrates associated with wetland soils. Snipe breed primarily in boreal forest regions and thus are found slightly north of the woodcock breeding range, with some areas of overlap in the eastern half of the continent. The breeding range of the snipe, however, extends westward to the Pacific coast and throughout most of Alaska, thus occupying a more extensive east-west range than the woodcock.

General references

Cade (1985); Dwyer et al. (1979); Dwyer and Storm (1982); Gregg (1984); National Geographic Society (1987); Owen et al. (1977); Sheldon (1967); Trippensee (1948).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A M A F	176 218		throughout range	Nelson & Martin, 1953	
	A M April A M May A M June	134.6 ± 2.9 SE 133.8 ± 5.8 SE 151.2 ± 9.5 SE		Maine	Dwyer et al., 1988	
	A M summer J M summer A F summer J F summer	145.9 140.4 182.9 168.8	127 - 165 117 - 152 162 - 216 151 - 192	central Massachusetts	Sheldon, 1967	
	A M fall J M fall A F fall J F fall	169 164 213 212		Minnesota	Marshall (unpubl.)	1
	at hatching	13.0	9 - 16	Wisconsin	Gregg, 1984	
Egg Weight (g)	at laying near hatching	18 - 19 14 - 16		Wisconsin	Gregg, 1984	
Chick Growth Rate (g/day)	M F	5.1 6.2		Maine	Dwyer et al., 1982	
Metabolic Rate (kcal/kg-day)	A F basal	115		s Michigan	Rabe et al., 1983b	2
(ilouality day)	A M basal A F basal	126 118			estimated	3
	A F free-living A F nesting	315 553		s Michigan	Rabe et al., 1983b	4
	A M free-living A F free-living	313 296	(148 - 662) (140 - 627)		estimated	5

Factors	Age/Sex/ Cond./Seas.		Mean			Rang (95% mean	CI of	Location	Reference	Note No.
Food Ingestion Rate (g/g-day)	A B w (eart diet)	inter hworm	0.77 0.1		0.11 -	1.43	Louisiana (captive)	Stickel et al., 1965		
Water Ingestion Rate (g/g-day)	A M A F		0.10 0.10						estimated	6
Inhalation Rate (m³/day)	A M A F		0.11 0.13						estimated	7
Surface Area (cm²)	A M A F		314 362						estimated	8
Dietary Composition		Spring	S	ummer	Fall		Winter	Location/Habitat (measure)	Reference	Note No.
earthworms Diptera Coleoptera Lepidoptera other animals plants				67.8 6.9 6.2 3.3 5.3				North America/NS (% volume; stomach contents)	Sperry, 1940	
earthworms beetle larvae grit (inorganic) other organic			1	58 10 31 1				Maine/fields (% wet weight; mouth esophagus, stomach, & proventriculus contents)	Krohn, 1970	9
earthworms other invertebra	ates						99+ <1	N Carolina/soybean fields (% wet weight; digestive tract)	Stribling & Doerr, 1985	
earthworms Coleoptera Hymenoptera							87 11 2	Alabama/NS (% volume; esophagus contents)	Miller & Causey, 1985	10

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A M inactive A M active A M singing	3.1 (median) 73.6 (median) 10.5 (median)	0.3 - 6.0 38.2 - 171.2 4.6 - 24.1	Pennsylvania/mixed forests with shrubs and fields	Hudgins et al., 1985	
	B B summer A F with brood	32.4 ± 27.6 SD 4.5	7 - 98	Wisconsin/woods, open areas, brush	Gregg, 1984	
Population Density (birds/ha)	B B winter B B winter B B winter	3.38 0.20 0.034		North Carolina/agricultural: untilled soy stubble untilled corn stubble rebedded corn fields	Connors & Doerr, 1982	
	nests in spring A M summer A F summer J B summer B B summer	0.21 (nests/ha) 0.035 0.056 0.125 0.223	0.026 - 0.046 0.037 - 0.074 0.108 - 0.143 0.190 - 0.250	Pennsylvania/mixed pine and hardwoods, open fields Maine/second growth forest, meadows, and ponds	Coon et al., 1982 Dwyer et al., 1988	
Clutch Size	1st clutch 2nd clutch	4 3.8 ± 0.42 SD 3.0 ± 0.67 SD	3 - 5	throughout range and habitats Maine/mixed forests, agricultural fields	Bent, 1927 McAuley et al., 1990	
Clutches/ Year		1 but renest if 1st lost		throughout range and habitats	McAuley et al., 1990	
Percent Nests Hatching		about 50		Maine/mixed forests, fields	McAuley et al., 1990	
Days Incubation		19 - 21		NS/NS	Mendall & Aldous, 1943; Pettingill, 1936	11
Age at Fledging		18 - 19 days		Wisconsin/woods, open areas, brush	Gregg, 1984	

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Age at Sexual Maturity	M F	< 1 year 1 year		throughout range and habitats	Sheldon, 1967	
Annual Mortality Rates	A M east A M central J M east J M central A F east A F central J F east J F central	65 ± 5.2 SD 60 ± 15 SD 80 ± 4.8 SD 64 ± 12 SD 51 ± 7.3 SD 47 ± 9.6 SD 64 ± 7.7 SD 69 ± 9.4 SD		eastern and central United States/NS	Dwyer & Nichols, 1982	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	early February early April		mid-March	Texas Maine	Whiting & Boggus, 1982 Dwyer et al., 1982	
Hatching	early February late February late March mid-April	early May mid-May	early June	Louisiana Virginia Connecticut Massachusetts Maine	Pettingill, 1936 Pettingill, 1936 Pettingill, 1936 Sheldon, 1967 Dwyer et al., 1982	1 1 1
Molt		August to early September		NS/NS	Owen & Krohn, 1973	12
Migration spring	mid-February March	April	early March	leaving North Carolina arriving in northern range	Connors & Doerr, 1982 Gregg, 1984	
fall	October late September		December mid-December	arriving North Carolina leaving Canada	Sheldon, 1967 Owen et al., 1977	

- 1 As cited in Sheldon (1967).
- 2 Metabolic rate estimated by authors from equation of Aschoff and Pohl (1970).
- Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and summer body weights from Nelson and Martin (1953).
- 4 Estimate of free-living metabolism based on energy budget model. Metabolism during nesting estimated for peak needs during egg-laying.
- Estimated using equation 3-37 (Nagy, 1987) and summer body weights from Nelson and Martin (1953).
- Estimated using equation 3-15 (Calder and Braun, 1983) and summer body weights from Nelson and Martin (1953).
- Estimated using equation 3-19 (Lasiewski and Calder, 1971) and summer body weights from Nelson and Martin (1953).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and summer body weights from Nelson and Martin (1953).
- 9 Grit comprised only 14 percent of total digestive tract contents volume.
- 10 Should provide a more accurate estimate of proportion of soft-bodied earthworms consumed than would including other portions of the digestive tract.
- 11 Cited in Trippensee (1948).
- 12 Cited in Owen et al. (1977).

References (including Appendix)

- Aldous, C. M. (1938) Woodcock management studies in Maine 1937. Trans. North Am. Wildl. Nat. Resour. Conf. 3: 839-846.
- Aschoff, J.; Pohl, H. (1970) Rhythmic variations in energy metabolism. Fed. Proc. 29: 1541-1552.
- Bent, A. C. (1927) Life histories of North American shore birds. Part 1. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 142.
- Britt, T. L. (1971) Studies of woodcock on the Louisiana wintering ground [master's thesis]. Shreveport, LA: Louisiana State University.
- Cade, B. S. (1985) Habitat suitability index models: American woodcock (wintering). U.S. Fish Wildl. Serv. Biol. Rep. 82(10.105).
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Connors, J. I.; Doerr, P. D. (1982) Woodcock use of agricultural fields in coastal North Carolina. In: Dwyer, T. J.; Storm, G. W., tech. coords. Woodcock ecology and management. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 139-147.
- Coon, R. A.; Williams, B. K.; Lindzey, J. S.; et al. (1982) Examination of woodcock nest sites in central Pennsylvania. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 55-62.
- Derleth, E. L.; Sepik, G. F. (1990) Summer-fall survival of the American woodcock in Maine. J. Wildl. Manage. 54: 97-106.
- Dunford, R. D.; Owen, R. B. (1973) Summer behavior of immature radio-equipped woodcock in central Maine. J. Wildl. Manage. 37: 462-469.
- Dwyer, T. J.; Nichols, J. D. (1982) Regional population inferences for the American woodcock. In: Dwyer, T. J.; Storm, G. L., tech. coords. Woodcock ecology and management. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 12-21.
- Dwyer, T. J.; Storm, G. L., eds. (1982) Woodcock ecology and management. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14.
- Dwyer, T. J.; Coon, R. A.; Geissler, P. H. (1979) The technical literature on the American woodcock 1927-1978. Laurel, MD: U.S. Fish Wildl. Serv., Migratory Bird and Habitat Research Laboratory.
- Dwyer, T. J.; Derleth, E. L.; McAuley, D. G. (1982) Woodcock brood ecology in Maine. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 63-70.

- Dwyer, T. J.; Sepik, G. F.; Derleth, E. L.; et al. (1988) Demographic characteristics of Maine woodcock population and effects of habitat management. Washington, DC: U.S. Fish Wildl. Serv. Res. Rep. 4.
- Dyer, J. M.; Hamilton, R. B. (1974) An analysis of feeding habits of the American woodcock (*Philohela minor*) in southern Louisiana. In: Fifth American woodcock workshop proceedings; December 3-5, 1974; Athens, GA. Athens, GA: University of Georgia.
- Godfrey, G. A. (1974) Behavior and ecology of American woodcock on the breeding range in Minnesota [Ph.D. dissertation]. Minneapolis, MN: University of Minnesota.
- Greeley, F. (1953) Sex and age studies in fall-shot woodcock (*Philohela minor*) from southern Wisconsin. J. Wildl. Manage. 17: 29-32.
- Gregg, L. (1984) Population ecology of woodcock in Wisconsin. Wis. Dept. Nat. Resour. Tech. Bull. No. 144; 51 pp.
- Gregg, L. E.; Hale, J. B. (1977) Woodcock nesting habitat in northern Wisconsin. Auk 94: 489-493.
- Hudgins, J. E.; Storm, G. L.; Wakeley, J. S. (1985) Local movements and diurnal-habitat selection by male woodcock in Pennsylvania. J. Wildl. Manage. 49: 614-619.
- Johnson, R.C.; Causey, M. K. (1982) Use of longleaf pine stands by woodcock in southern Alabama following prescribed burning. In: Dwyer, T. J.; Storm, G. W., tech. coords. Woodcock ecology and management. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 120-125.
- Keppie, D. M.; Redmond, G. W. (1985) Body weight and the possession of territory for male American woodcock. Condor 87: 287-290.
- Keppie, D. M.; Redmond, G. W. (1988) A review of possible explanations for reverse size dimorphism of American woodcock. Can. J. Zool. 66: 2390-2397.
- Krohn, W. B. (1970) Woodcock feeding habits as related to summer field usage in central Maine. J. Wildl. Manage. 34: 769-775.
- Krohn, W. B.; Martin, F. W.; Burnham, K. P. (1974) Band-recovery distribution and survival estimates of Maine woodcock. Proc. Am. Woodcock Workshop 5: 1-8.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.

- Martin, F. W.; Williams, S. O.; Newsom, J. D.; et al. (1969) Analysis of records of Louisiana-banded woodcock. Proc. Ann. Conf. Southeast. Assoc. Game and Fish Comm. 23: 85-96.
- McAuley, D. G.; Longcore, J. R.; Sepik, G. F. (1990) Renesting by American woodcock (*Scolopax minor*) in Maine. Auk 107: 407-410.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Mendall, H. L.; Aldous, C. M. (1943) The ecology and management of the American woodcock. Orono, ME: Maine Coop. Res. Unit, University of Maine; 201 pp.
- Miller, D. L.; Causey, M. K. (1985) Food preferences of American woodcock wintering in Alabama. J. Wildl. Manage. 49: 492-496.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Nelson, A. L.; Martin, A. C. (1953) Gamebird weights. J. Wildl. Manage. 17: 36-42.
- Norris, R. T.; Buele, J. D.; Studholme, A. T. (1940) Banding woodcocks on Pennsylvania singing grounds. J. Wildl. Manage. 4: 8-14.
- Owen, R. B.; Galbraith, W. J. (1989) Earthworm biomass in relation to forest types, soil, and land use: implications for woodcock management. Wildl. Soc. Bull. 17: 130-136.
- Owen, R. B.; Krohn, W. B. (1973) Molt patterns and weight changes of the American woodcock. Wilson Bull. 85: 31-41.
- Owen, R. B.; Morgan, J. W. (1975) Summer behavior of adult radio-equipped woodcock in central Maine. J. Wildl. Manage. 39: 179-182.
- Owen, R. B.; Anderson, J. M.; Artmann, J. W.; et al. (1977) American woodcock. In: Sanderson, G. C., ed. Management of migratory shore and upland game birds in North America. Washington, DC: Int. Assoc. Fish Wildl. Agencies; pp. 147-175.
- Pettingill, O. S., Jr. (1936) The American woodcock. Boston Soc. Nat. Hist. Mem. 9(2).
- Rabe, D. L.; Prince, H. H.; Beaver, D. L. (1983a) Feeding-site selection and foraging strategies of American woodcock. Auk 100: 711-716.
- Rabe, D. L.; Prince, H. H.; Goodman, E. D. (1983b) The effect of weather on bioenergetics of breeding American woodcock. J. Wildl. Manage. 47: 762-771.

- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Sheldon, W. G. (1967) The book of the American woodcock. Amherst, MA: University of Massachusetts Press.
- Sperry, C. (1940) Food habits of a group of shore birds; woodcock, snipe, knot, and dowitcher. U.S. Dept. Int., Bur. Biol. Survey, Wildl. Res. Bull. 1; 37 pp.
- Stickel, W. H.; Hayne, D. W.; Stickel, L. F. (1965) Effects of heptachlor-contaminated earthworms on woodcocks. J. Wildl. Manage. 29: 132-146.
- Stribling, H. L.; Doerr, P. D. (1985) Nocturnal use of fields by American woodcock. J. Wildl. Manage. 49: 485-491.
- Trippensee, R. E. (1948) American woodcock. Wildlife management. New York, NY: McGraw-Hill; pp. 323-332.
- Tufts, R. W. (1940) Some studies in bill measurements and body weights of American woodcock (*Philohela minor*). Can. Field-Nat. 54: 132-134.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Wetherbee, D. K.; Wetherbee, N. S. (1961) Artificial incubation of eggs of various bird species and some attributes of neonates. Bird Banding 32: 141-159.
- Whiting, R. M.; Boggus, T. G. (1982) Breeding biology of American woodcock in east Texas. In: Dwyer, T. J.; Storm, G. W., tech. coords. Woodcock ecology and management. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 14; pp. 132-138.

2.1.11. Spotted Sandpiper (sandpipers)

Order Charadriiformes, Family Scolopacidae. The family Scolopacidae includes numerous species of shorebirds, e.g., sandpipers, tattlers, knots, godwits, curlews, yellowlegs, willets, and dowitchers. Those known as sandpipers tend to be small with moderately long legs and bills. Most sandpipers forage on sandy beaches and mudflats; a few utilize upland areas. They feed almost exclusively on small invertebrates, either by probing into or gleaning from the substrate. Most species are highly migratory, breeding in arctic and subarctic regions and either wintering along the coasts or in southern latitudes and the southern hemisphere; therefore, many are only passage migrants throughout most of the United States. Scolapids range in size from the least sandpiper (11.5 cm bill tip to tail tip) to the long-billed curlew (48 cm).

Selected species

The spotted sandpiper (*Actitis macularia*) (19 cm) is a very common summer resident of freshwater and saltwater bodies throughout most of the United States. These sandpipers are most often encountered singly but may form small flocks. Most winter in the neotropics.

Body size. Females (approximately 50 g) are significantly larger than males (approximately 40 g) (Oring and Lank, 1986).

Habitat. Spotted sandpipers breed along the edges of bodies of water, usually in open habitats, from the northern border of the boreal forest across North America, south to the central United States (Oring and Lank, 1986). They require open water for bathing and drinking, semi-open habitat for nesting, and dense vegetation for breeding (Bent, 1929; Oring et al., 1983).

Food habits. In coastal areas, spotted sandpipers search the beach and muddy edges of inlets and creeks, wading less frequently than most sandpipers; inland they feed along the shores of sandy ponds and all types of streams, sometimes straying into meadows, fields, and gardens in agricultural areas (Bent, 1929). Their diet is composed primarily of terrestrial and marine insects (Bent, 1929). While adult flying insects comprise the bulk of the diet, crustaceans, leeches, molluscs, small fish, and carrion also are eaten (Oring et al., 1983). Young feed themselves immediately after hatching, concentrating on small invertebrates (Oring and Lank, 1986). During insect outbreaks, sandpipers will forage in wooded areas near water, and they have been observed eating eggs and fish on occasion (Oring, pers. obs.).

Molt. Partial prenuptial molt of body plumage occurs in March and April, while the postnuptial molt begins by August with the body feathers and ends anywhere from October to April with the loss of the primary flight feathers (Bent, 1929).

Migration. Spotted sandpipers generally migrate in small flocks or solitarily (National Geographic Society, 1987). They winter from southern United States to northern Chile, Argentina, and Uraguay (Oring and Lank, 1986), and breed across North

America, north from Virginia and southern California (National Geographic Society, 1987). In the spring, females arrive at the breeding grounds earlier than males (in one study, by about 2 weeks; Oring and Lank, 1982).

Breeding activities and social organization. The primary consideration for nesting sites is proximity to water, and spotted sandpipers have been known to build their ground nests in such diverse conditions as depressions in volcanic rock and strawberry patches (Bent, 1929). Spotted sandpipers are polyandrous (i.e., a single female lays eggs for multiple males), with males supplying most of the incubation and parental care (Oring, 1982). Thus reproduction is limited by the number of males present (Lank et al., 1985). Spotted sandpipers lay a determinate clutch of four eggs. Females may lay several clutches in a year, often a dozen eggs per season (Maxson and Oring, 1980). Egg laying begins between late May and early June in Minnesota (Lank et al., 1985), and males incubate after the third egg is laid (Oring et al., 1986). Females sometimes incubate and brood when another male is not available (Maxson and Oring, 1980). Parents brood small chicks and protect them with warning calls or by distracting or attacking predators (Oring and Lank, 1986).

Home range and resources. Although a variety of vegetation types are used, nests usually are placed in semi-open vegetation near the edge of a lake, river, or ocean (Oring et al., unpubl., as cited in Oring et al., 1983; McVey, pers. obs.). The suitability of nesting habitat varies from year to year in some locations due to levels of precipitation and predators (Oring et al., 1983).

Population density. Spotted sandpiper nesting densities have been studied well at only one location, on Little Pelican Island, Leech Lake, Minnesota. At this location, densities ranged from 4 to 13 females per hectare and 7 to 20 males per hectare over a 10-year period, depending on weather and other conditions (Oring et al., 1983).

Population dynamics. Females may lay one to six clutches for different males over one season (Oring et al., 1984), averaging 1.3 to 2.7 mates per year (Oring et al., 1991b). Female mating and reproductive success increase with age, but male success does not (Oring et al., 1991b). Lifetime reproductive success is most affected by fledging success and longevity for both males and females (Oring et al., 1991a).

Similar species (from general references)

- The solitary sandpiper (*Tringa solitaria*) is usually seen singly in freshwater swamps or rivers. Present over much of the United States during annual migrations, this average-sized sandpiper (18 cm) winters along the southeast and Gulf coasts.
- The western sandpiper (*Calidris mauri*) is a small sandpiper (13 cm), common on mudflats and sandbars, that winters on both the Atlantic and Pacific shores of the United States.

- The least sandpiper (*Calidris minutilla*), the smallest of this group (11 cm), is common in winter on salt marshes and muddy shores of rivers and estuaries in coastal areas across the United States.
- The semipalmated sandpipers (Calidris pusilla) are small birds (13 cm) seen in the United States primarily during migration and rarely wintering on Florida coasts.
- Most other members of the family Scolopacidae forage by gleaning.

General references

Oring and Lank (1986); Lank et al. (1985); National Geographic Society (1987); Oring et al. (1991a, 1991b).

Spotted Sandpiper (Actitis macularia)

Factors	Age/S Cond.	ex/ /Seas.	Mean		Range or (95% Cl of mean)		mean)	Location	Reference	Note No.
Body Weight (g)	A F sp A M s		47.1 37.9		43 - 50 34 - 41			Minnesota island	Maxson & Oring, 1980	
Metabolic Rate (kcal/kg-day)	A F pre-breed A F laying A F incubating A M pre-breed A M incubating A M brooding A F free-living A M free-living			0 3 5 6	(202 - 937) (213 - 994)			Minnesota	Maxson & Oring, 1980 estimated	2
Food Ingestion Rate (g/g-day)										3
Water Ingestion Rate (g/g-day)	A F A M		0.1 0.1						estimated	4
Inhalation Rate (m³/day)	A F A M		0.039 0.033						estimated	5
Surface Area (cm²)	A F A M		131 113						estimated	6
Dietary Composition Spring			Summer	Fall		Winter	Location/Habitat (measure)	Reference	Note No.	
mayflies midges			√ √				Minnesota/island in lake	Maxson & Oring, 1980		
Population Dynamics	Age/Sex Cond./Seas.		Mean		Range		Location/Habitat	Reference	Note No.	
Territory Size (ha)			approx. 0.25					NS/NS	Maxson & Oring, 1980	

Spotted Sandpiper (Actitis macularia)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (N/ha)	A F summer A M summer	10 13.9	3.8 - 12.5 7.5 - 20.0	Minnesota/island in lake	Oring et al., 1983	
Clutch Size		4	3 - 5	NS/NS	Bent, 1929; Oring et al., 1983	7
Clutches/Year			1 - 6	Minnesota/NS	Oring et al., 1983	
Days Incubation		18 to 24		NS/NS	Oring, unpublished	
Age at Fledging		approximately 18 days		NS/NS	Oring et al., 1991a	
Number Fledge per Nest That Hatches		1.83	0.58 - 2.76	Minnesota/island in lake	Oring et al., 1984	
Number Fledge per Successful Nest		2.58	1.67 - 2.91	Minnesota/island in lake	Oring et al., 1984	
Age at Sexual Maturity	F M	1 year 1 year		Minnesota/island in lake	Oring et al., 1983	
Annual Mortality Rates (percent)	F M	approx. 31 approx. 30		Minnesota/island in lake	Oring et al., 1983; Oring & Lank, 1982; Oring, unpublished	
Longevity	AF	3.7 years		Minnesota/island in lake	Oring et al., 1983	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early May	late May - early June		Minnesota	Lank et al., 1985	
Hatching	early June	late June		Minnesota	Lank et al., 1985	

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Spotted Sandpiper

Spotted Sandpiper (Actitis macularia)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Molt fall spring	August	March - April	October	NS	Bent, 1929 Bent, 1929	
Migration females males	late June early July	early - mid-July mid-July		Minnesota	Lank et al., 1985	

- 1 Estimated by authors; allometric model not specified.
- 2 Estimated using equation 3-37 (Nagy, 1987) and body weights from Maxson and Oring (1980).
- 3 See Chapters 3 and 4 for methods of estimating food ingestion rates; also see Section 4.1.3 and Table 4-4 for sediment ingestion rates for sandpipers.
- 4 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Maxson and Oring (1980).
- 5 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Maxson and Oring (1980).
- Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Maxson and Oring (1980).
- 7 Spotted sandpipers are determinate layers, with a clutch size of four eggs. Clutches with fewer eggs are not complete or have lost eggs; larger clutches are the result of more than one female laying in a nest.

References (including Appendix)

- Bent, A. C. (1929) Life histories of North American shore birds. Part 2. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 146.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.
- Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.
- Kuenzel, W. J.; Wiegert, R. G. (1973) Energetics of a spotted sandpiper feeding on brine fly larvae (Paracoenia; Diptera: Ephydridae) in a thermal spring community. Wilson Bull. 85: 473-476.
- Lank, D. B.; Oring, L. W.; Maxson, S. J. (1985) Mate and nutrient limitation of egg-laying in a polyandrous shorebird. Ecology 66: 1513-1524.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.
- Maxson, S. J.; Oring, L. W. (1980) Breeding season time and energy budgets of the polyandrous spotted sandpiper. Behaviour 74: 200-263.
- Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.
- National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.
- Oring, L. W. (1982) Avian mating systems. In: Farner, D. S.; King, J. R., eds. Avian biology, v. 6. New York, NY: Academic Press; pp. 1-92.
- Oring, L. W.; Lank, D. B. (1982) Sexual selection, arrival times, philopatry and site fidelity in the polyandrous spotted sandpiper. Behav. Ecol. Sociobiol. 10: 185-191.
- Oring, L. W.; Lank, D. B. (1986) Polyandry in spotted sandpipers: the impact of environment and experience. In: Rubenstein, D. I.; Wrangham, R. W., eds. Ecological aspects of social evolution birds and mammals; pp. 21-42.
- Oring, L. W.; Lank, D. B.; Maxson, S. J. (1983) Population studies of the polyandrous spotted sandpiper. Auk 100: 272-285.
- Oring, L. W.; Lank, D. B.; Maxson, S. J. (1984) Mate and nutrient limitation of breeding in the polyandrous spotted sandpiper (abstract only). Am. Zool. 24: 60A.

- Oring, L. W.; Fivizzani, A. J.; Halawani, M. E. (1986) Changes in plasma prolactin associated with laying and hatch in the spotted sandpiper. Auk 103: 820-822.
- Oring, L.W.; Colwell, M.A.; Reed, J.M. (1991a) Lifetime reproductive success in the spotted sandpiper (*Actitis macularia*): sex differences and variance components. Behav. Ecol. Sociobiol. 28: 425-432.
- Oring, L.W.; Reed, J.M.; Colwell, M.A.; et al. (1991b) Factors regulating annual mating success and reproductive success in spotted sandpipers (*Actitis macularia*). Behav. Ecol. Sociobiol. 28: 433-442.
- Palmer, R. S. (1949) Maine birds. Bull. Mus. Comp. Zool. Harvard No. 102.
- Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.
- Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.
- Walsberg, G. E.; King, J.R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.
- Zar, J. H. (1968) Standard metabolism comparisons between orders of birds. Condor 10: 278.